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JOHN WILLIAM HARDIMAN
University of New Hampshire, Durham

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INBREEDING IN JAPANESE QUAIL SELECTED FOR THREE WEEK BODY WEIGHT

by

JOHN WILLIAM HARDIMAN

B.A., State University of New York College
at Cortland, 1970

A THESIS

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This thesis has been examined and approved.

Thesis director, Walter M. Collins, Prof. of Animal Sciences and Genetics

Willard E. Urban, Jr., Asso. Prof. of Biometrics and Genetics

Yun Tzu Kiang, Asso. Prof. of Plant Science and Genetics

Frank K. Hoornbeek, Asso. Prof. of Zoology and Genetics

Winthrop C. Skoglund, Prof. and Chairman of Animal Sciences

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Date

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To my Mother and Father

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

INBREEDING IN JAPANESE QUAIL SELECTED FOR THREE WEEK BODY WEIGHT

by

JOHN WILLIAM HARDIMAN

Coefficients of inbreeding for all individuals in each of four lines of Japanese quail were calculated by computer using the variance-covariance method. Two lines (1 and 4), initially, were family selected for three week body weight and two (2 and 3) were designated as unselected control lines. The experiment ran for 36 generations. Selection was relaxed in G_{27} in line 1 and in G_{29} in line 4. Each line was reproduced by 50 pair matings each generation and full-sib matings were avoided.

Per generation increases in inbreeding over the generations during which selection was practiced were 1.2 and 1.5 percent in lines 1 and 4, respectively, and 0.4 percent in the control lines. During relaxed selection, inbreeding rates declined to 0.6 percent per generation in line 1 and 0.3 percent in line 4. In G_{36}, inbreeding was 34 and 41 percent in lines 1 and 4 compared to 13 and 12 percent in lines 2 and 3, respectively.

Effective population size was used to estimate theoretical rate and magnitude of inbreeding each generation. In the control lines, these theoretical inbreeding rates were only slightly

higher than those calculated by the variance-covariance method. In the selected lines, however, theoretical rates were 0.20 and 0.28 percent per generation greater, respectively, than those calculated by the variance-covariance method. The formula for effective population size made no adjustment for the avoidance of full-sib matings and, therefore, greatly overestimated inbreeding in the family selected lines.

The shapes of distributions of coefficients of inbreeding were studied for each line each generation. Distributions were least normal in the control lines where rate of inbreeding was low and more nearly normal in the selected lines where inbreeding accrued more rapidly. All distributions were positively skewed but much more so in the control than in the selected lines. In the control lines distributions were almost all flat-topped but in the selected lines were often peaked over the intermediate generations. A change in inbreeding rate sometimes resulted in changes in distribution shape in the selected lines.

Coefficients for the regression of each of eight traits (Y) on inbreeding (X) were obtained within-generation for each line. Within-generation regression coefficients varied greatly in magnitude among generations but generally did not change significantly over time. Pooled regression coefficients were obtained for each line by pooling within-generation corrected sums of squares (Σx^2, Σy^2) and crossproducts (Σxy) over all generations. Pooled regression coefficients were consistently negative for three week body weight (TW), adult body weight (AW),

egg weight (EW), egg production (EP), hatchability of fertile eggs (HFE), hatchability of total eggs (HTE) and family size (FS) but sometimes were positive for fertility (FE). Magnitude of inbreeding depression varied greatly among lines and was usually least in line 2. Changes in performance with inbreeding for the two control lines when averaged usually were very similar to the average changes upon inbreeding found for the selected lines. Changes in performance with inbreeding averaged over all lines were generally similar to or less than estimates of the effects of inbreeding reported in other experiments. In this experiment, traits normally having high heritabilities (TW, AW and EW) were depressed to a lesser extent from inbreeding than those with low heritabilities (HFE, HTE and FE).

INTRODUCTION

Inbreeding is the mating, within a population, of individuals more closely related to each other than the average relationship within that population (Lush, 1948). Knowledge of the degree of inbreeding in an artificially selected population is important since continued inbreeding is often accompanied by general decreases in vigor (Falconer, 1960) and because highly inbred lines are sources of phenotypically and genetically similar commercial or experimental animals. Studies to determine magnitudes of effects of inbreeding on a number of economic and fitness traits and the feasibility of establishing inbred lines for a number of agricultural and experimental animals have been conducted.

Among poultry species, chickens have been the most frequent subjects of inbreeding studies. Continuous inbreeding has usually been accompanied by increases in mortality and in age at sexual maturity and by decreases in egg production, fertility and hatchability. Body weight and egg weight have been depressed relatively less.

Relatively few studies have been conducted on inbreeding in domesticated Japanese quail. This seems surprising since quail are an avian species and generations accrue at a rate approximately four times as rapidly as in chickens. In most of these experiments, responses of specific traits to successive full-sib matings were investigated. Traits depressed by

inbreeding in chickens were also depressed in quail. Again, body weight and egg weight were depressed to a lesser degree than the other traits.

Investigations into the shapes of inbreeding distributions have not previously been reported in the literature. Thus of major interest in this research, were distributions of individual coefficients of inbreeding. The shapes of these distributions may be affected by rate or magnitude of inbreeding within a line and may vary between lines and over time. If distribution shape could be predicted from level or rate of inbreeding, the proportion of individuals in a line with different degrees of inbreeding might be estimated without constructing frequency distributions of inbreeding values.

Response of quail to inbreeding has not been studied over large numbers of generations or where rates of inbreeding were low. The effect of inbreeding on a particular trait may change as the level of inbreeding increases with time. Depression of total litter weight in pigs at farrowing, weaning and 154 days of age due to inbreeding of the dam was relatively greater during later stages of inbreeding (Bereskin et al., 1968). Pendlebury and Kidwell (1974), on the other hand, observed that male competitive mating ability and mating rate in Drosophila melanogaster declined less per unit inbreeding after inbreeding went beyond 25 percent. Under conditions in which inbreeding accrued slowly, natural selection opposed inbreeding depression (Eisen and Hanrahan, 1974). Therefore, it is of interest and importance to investigate the impact of inbreeding on various economic and

fitness traits in quail at relatively high levels of inbreeding and after many generations of selection.

The commercial breeder is interested in differences in the rate and level of inbreeding observed under different mating systems. Information regarding the accuracy of estimates of inbreeding based upon effective population size would be of value since this method involves less work than calculating a Wright's coefficient of inbreeding for each individual. Breeders might wish to know the proportion of individuals in a line whose inbreeding is below a specified value (e.g., the mean inbreeding). It would be expedient if this could be estimated from the rate of inbreeding per se in such a line. Selection programs might be geared to compensate for expected decreases in performance of specific traits with inbreeding and especially for those traits in which the effects of inbreeding are compounded at higher levels.

REVIEW OF LITERATURE

Measurement of Inbreeding

Methods have been developed by which the degree of inbreeding within a population may be measured quantitatively. Formulae have been derived for the rate at which organisms become homozygous through continuous self-fertilization (Jennings, 1912) or continued full-sib matings (Jennings, 1914). Pearl (1917a, 1917b) described a coefficient of inbreeding, Z, which expressed the actual amount of inbreeding relative to the maximum amount of inbreeding possible (i.e., that resulting from full-sib matings only) for each ancestral generation as well as the entire pedigree of a particular inbred individual. However, this coefficient did not produce accurate results for all mating systems.

Matings between individuals with common ancestry result in some correlation between the genes in their uniting gametes (Wright, 1921). This correlation, referred to as Wright's coefficient of inbreeding (F) was selected by Wright (1922) to estimate the degree of inbreeding among the offspring of such matings. It estimates any individual's average increase in homozygosity over that existing among all individuals in the base generation of his pedigree and is written as

$$F_X = \Sigma \left[(\tfrac{1}{2})^{n+n'+1} \ (1+F_A) \right].$$

Where F_X is the inbreeding coefficient of the inbred individual, n and n' are the number of generations from sire and dam,

respectively, to a common ancestor and F_A is the inbreeding coefficient of that common ancestor. The factor ½ is the probability at each meiotic segregation in the chain of inheritance between the sire and the dam that an individual will inherit a gene identical by descent from a common ancestor. The plus one in the formula refers to the additional 50 percent probability that a particular common ancestor gave replicates of one of its genes to both of his immediate offspring in the path being traced. F_X is calculated by tracing all paths to each common ancestor. Malecot (1948) defined this coefficient as the probability of two genes being identical by descent at a given locus within an individual. Values of F range from 0.0 to 1.0.

Wright's coefficient of inbreeding measures only the degree of progress toward complete homozygosity, while the magnitude of the inbreeding at any time is equal to the sum of this progress plus the degree of homozygosity in the base generation. The degree of inbreeding in the base generation of a population is often assumed to be zero (i.e., all individuals are assumed heterozygous at all loci). If this is true, an individual F value of 0.5 in a later generation would mean that the probability of homozygosity at any one locus would be 50 percent. If, however, the degree of homozygosity in the base population was, for example, 50 percent, then the degree of homozygosity of an individual with an F value of 0.5 would be 75 percent according to the formula (Wright, 1922):

$$\text{percent homozygosity} = \tfrac{1}{2}(1+F) \times 100.$$

Obviously, inaccuracy in estimating the inbreeding in the base generation of a population decreases the accuracy of estimates of the magnitude of inbreeding in later generations. Also, should the degree of homozygosity fall below that of a base population in which inbreeding was assumed to be zero, the inbreeding values cannot become negative (Allen, 1965).

Wright (1921) calculated algebraically the percentage of homozygosity arising under each of 11 different regular systems of inbreeding ranging from self-fertilization to second cousin matings. Haldane (1937, 1955) and Fisher (1949) obtained the same results using matrix mathematics. The percentage of homozygosity resulting from inbreeding for sex-linked genes (assuming heterogametic males carrying one sex-linked gene and homogametic females carrying two sex-linked genes) was calculated by Wright (1933) and Haldane (1955). Under similar mating systems, the percentage of homoztgosity was usually greater for sex-linked than for autosomal genes. Mating systems using only one member of the heterogametic sex per generation produced equal degrees of homozygosity for both autosomal and sex-linked genes. Schnell (1961), Kimura (1963), Shikata (1965) and Van Aarde (1974) used probability theory to derive formulae for determining the probability of variable numbers of linked loci all being homozygous. The probability of all of a set of linked loci being homozygous more closely approaches the probability of a single locus being homozygous as the degree of linkage increases.

Rates of inbreeding can also be estimated for populations where breeding structure and population size are known but the exact relationships between mating individuals are not. Effective population size, N_e, (the size of an ideal population with the same inbreeding or variance properties as the actual population being studied (Crow, 1964)) can be calculated for such populations and the average inbreeding per generation determined from this since $\Delta F = \frac{1}{2N_e}$ (Falconer, 1960). This method does not, however, yield inbreeding coefficients for each individual or take into account the use of a breeder in more than one generation (overlapping generations).

The calculation of Wright's coefficient of inbreeding for large, complex pedigrees by manually tracing closed paths is time consuming and prone to error. The use of a sampling technique is one way to reduce the number of calculations required for a population and covariance tables, geometric symbols, matrices and computer programs have been used to simplify them. A method of estimating inbreeding coefficients for large populations by tracing the pedigrees of several families chosen at random was introduced by Wright (1925). Hazel and Lush (1950) used punched electronic data processing cards to simplify the tracing of paths within a pedigree. Covariance charts and tables were used in place of pedigrees for calculating inbreeding coefficients from a specified base generation onward by Emik and Terrill (1949), Cruden (1949) and Plum (1954). Kudo (1962) developed a method of calculating these coefficients particularly applicable to

human pedigrees which used pedigree sheets filled with geometric symbols instead of numbers and extended this method to sex-linked genes (Kudo and Sakaguchi, 1963). The use of symbols greatly reduced the chance of mathematical error. Maryyama and Yasuda (1970) used graph theory and matrices to determine inbreeding. Their method did not require that calculations proceed from a specified base generation onward. Mange (1964) and Rehfeld et al. (1967) described computer programs for calculating inbreeding coefficients for up to seven overlapping generations. The methods of Emik and Terrill (1949), Kudo (1962) and Cruden (1949) were programmed for the computer by Hoen and Grandage (1960), MacCluer et al. (1967) and Li and Roderick (1970), respectively. Inbreeding coefficients are part of the output for a Population Search Program reported by MacLean (1969) and for a computer program for dioecious plants written by Lowe (1972).

Theoretical Effects of Inbreeding

Inbreeding changes gene and genotypic frequencies, may reduce mean phenotypic values and changes the genetic variance within and between lines. Much of the theory concerning these effects is reviewed by Falconer (1960) and is summarized here.

There is an increase in the frequency of each homozygote due to inbreeding of $p_o q_o F$ where p_o and q_o are the initial frequencies of two different alleles at a particular locus. Correspondingly there is a decrease of $2p_o q_o F$ in the frequency of the heterozygote. Therefore, continuous inbreeding may result in the fixation, or loss, of a particular allele due to chance.

The combined probability of the fixation or loss of such an allele is approximately equal to the inbreeding coefficient.

If there is dominance among alleles responsible for superior reproductive capacity or physiological efficiency, a decrease in the proportion of heterozygotes due to inbreeding may result in poorer performance in these characters. This reduction in mean phenotypic value (inbreeding depression) depends not only on the presence of dominance but also on a preponderance of dominance in one direction. According to the dominance hypothesis (Crow, 1952), those genes increasing trait values are assumed to be mostly dominant while those reducing these values are assumed to be mostly recessive. The lower the frequency of these recessive genes prior to inbreeding, the greater is their relative increase upon inbreeding.

The overdominance hypothesis (Crow, 1952), on the other hand, states that inbreeding depression may result from overdominance (the heterozygote is superior in performance to either homozygote) and one would expect the degree of inbreeding depression due to overdominance to be greater than that for either partial or complete dominance (Li, 1963). Crow (1952) suggested that inbreeding depression is explained mainly by the dominance hypothesis. He further proposed that the overdominance hypothesis is of greater value than the dominance hypothesis for explaining the increase in vigor, over that of a base population, which results from the crossing of lines derived from that population.

If the products of different gene loci affecting a particular trait depressed by inbreeding combine additively, the relationship between degree of inbreeding and change in the mean of that trait should be linear. When, however, both dominance and epistasis are present, this relationship may be non-linear (Crow and Kimura, 1970). Genes which are dominant in their epistatic effect should decrease the mean while those which are recessive should increase the mean upon inbreeding (Lush, 1948). Inbreeding depression should be least when the rate of inbreeding is slow and natural selection has the opportunity to remove individuals possessing deleterious homozygous combinations of genes from the population (Falconer, 1960). Van Aarde (1974) showed mathematically that linkage should accelerate any effects attributable to continued inbreeding (i.e., inbreeding depression). Biemont et al. (1974) proposed a molecular theory of inbreeding and heterosis based on the existence of interactions between gametic genomes in the zygote.

Inbreeding populations become subdivided into series of inbreeding families or lines. Increasing the degree of inbreeding decreases genetic variance within lines but increases genetic variance between lines in the absence of non-additive genetic variance and selection. If V_G is the variance attributable to additive genes in the base population and F is the level of inbreeding in a population, then variance between and within lines is expected to change by the following amounts:

Between lines	$2FV_G$
Within lines	$(1-F)V_G$
Total	$(1+F)V_G$

Heritability, the ratio of additive genetic variance to phenotypic variance, is expected to decrease with increased inbreeding within small populations in the absence of selection and non-additive genetic variance.

If there is some degree of dominance among genes affecting a specific character, the change in the genetic variance of this character within and between lines is dependent upon the initial frequencies of those genes. For example, Robertson (1952) showed that for recessive genes at low frequencies in small populations, within line variance increased during the early stages of inbreeding to a maximum where F was approximately 0.5. Lagervall (1961) examined theoretically the response of additive and dominance genetic variances to increasing inbreeding for genes with different frequencies and different degrees of dominance for one locus with two to three alleles. The additive genetic variance increased by 1+F as F increased when there was no dominance or epistasis. The same increase was found when there was dominance (with or without epistasis V_{AA} or V_{AAA}) and gene frequencies were all 0.5. For gene frequencies other than 0.5, the increase in additive genetic variance upon inbreeding was progressively less than 1+F for increasing degrees of dominance. The dominance variance was greater for higher degrees of dominance. There was either a

curvilinear decrease or an increase to a maximum followed by a decrease for the dominance variance as inbreeding increased.

Factors Affecting Rates of Inbreeding in Closed Populations

The rate of inbreeding in natural and experimental populations is dependent mainly upon the mating system and, under random mating, upon population size. Wright (1931) described the calculation of inbreeding for randomly mating populations of size N and later (Wright, 1933) calculated inbreeding for a variety of non-random mating systems. In all cases, the rate of inbreeding increased as population size decreased. In non-random mating populations, inbreeding accrues most rapidly among plants under self-fertilization and only about half as rapidly among animals under full-sib or parent-offspring matings. The latter system of mating has a somewhat higher rate of inbreeding for both autosomal (Fisher, 1959) and sex-linked (Wright, 1933) genes than does full-sib mating.

Rates of inbreeding may be affected by selection, the degree of dominance, linkage and by mutation. Robertson (1961) noted that selection per se increases the rate of approach to homozygosity for all loci. Hayman and Mather (1953), on the other hand, showed that selection for heterozygotes within any one line helps decrease the rate of inbreeding but does not arrest it. If, however, selection operates between a series of lines, the approach to complete homozygosity may be reduced or stopped completely depending on the intensity of selection

against the homozygote. Miller et al. (1971) found that inbreeding proceeded at the greatest rate under genotypic selection (selection for individuals with the largest genotypic values), at an intermediate rate under phenotypic selection (selection for individuals with the largest phenotypic values) and at the slowest rate when individuals were chosen at random. In addition, the rate of inbreeding was highest, intermediate and lowest in the case of partial dominance, complete dominance and overdominance, respectively.

Bereskin (1972) examined the effects of intensity of selection, population size and mode of gene action on rate of inbreeding by use of computer simulation. The rate of increase in inbreeding was lowest under selection of low intensity, in populations of large size and where non-additive gene action was involved. The results of a computer simulation study by Gill and Clemmer (1966) indicated that both selection and linkage could increase inbreeding. A randomization error in their program was corrected by Bogyo and Ting (1968) who averaged results obtained over three different levels and two different methods of selection and found that only under very high levels of linkage (99 percent) would inbreeding increase. Miller et al. (1971), also using computer simulation, studied the effects of several modes of selection, degrees of dominance and levels of linkage on inbreeding. Only for the case of partial dominance were populations with tighter linkage more inbred. In populations inbred for long periods of time, mutation may be of some

importance in providing a source of heterogeneity (Falconer, 1960).

Certain mating systems are designed to minimize the rate of inbreeding. Kimura and Crow (1963) compared maximum avoidance, circular individual and circular pair mating systems as to their rates of decrease in heterozygosity. The circular individual mating system showed the greatest initial decrease in heterozygosity but maintained the highest degree of heterozygosity in later generatio . Gowe et al. (1959) showed that choosing equal numbers of males and females as breeders and at least one breeder from each family each generation doubled the effective population size and reduced the rate of inbreeding. Robinson (1965) examined rates of inbreeding under four different mating systems designed to minimize inbreeding. Mating systems were: (1) selection and mating of individuals at random, (2) selection at random and mating so as to avoid full-sib matings, (3) one male and one female chosen at random from each family and mated at random and (4) one male and one female chosen at random from each family and mated so as to avoid full-sib matings. Choosing one male and one female at random from each family while also avoiding full sib-matings, system (4), resulted in a smaller percentage of homozygosity than any of the other mating systems except after relatively long periods of time (e.g., 270 generations for populations containing 50 families). System (1) in which individuals were selected and mated at random always produced the highest degree of homozygosity.

Effects of Inbreeding on Various Traits in Domesticated Chickens

Studies into the effects of inbreeding on fitness and economic traits in the domestic chicken indicate generally that increases in inbreeding reduce mean values of several fitness traits but have little effect on body weight and egg weight. Coefficients for the linear regressions of these trait values on inbreeding were taken from the literature on chickens and Japanese quail and are presented in Table 1. They are estimates of the changes in trait values per one percent increase in inbreeding. Coefficients presented in this table were obtained from selection as well as inbreeding experiments when (1) the selection was not believed to have influenced the trait under consideration or when (2) responses to inbreeding were estimated by within-generation regressions. All regression coefficients were rounded to two decimals to facilitate reading and interpretation. The breed of chicken is not listed in this table and is not always specified in this section since different breeds responded similarly to increases in inbreeding.

Goodale (1927) and Waters and Lambert (1936) reported that age at sexual maturity in the chicken did not change with relatively high levels of inbreeding but others have shown that age at sexual maturity increases as inbreeding increases (Dunn, 1923; Hays, 1924; Jull, 1933; Hays, 1935; Shoffner, 1948; Hays and Talmadge, 1949; Blow and Glazener, 1953; Morris, 1962). Selection for early maturity has usually been successful in

Table 1. - Linear regression coefficients for the regression of trait value (Y) on inbreeding coefficient (X) for domesticated chickens and Japanese quail

Trait	Specie		Reference[h]	
	Domesticated chicken	Japanese quail	Chicken	Quail
Age of female at sexual maturity (days)	.60*, .32*, .40	.1†, .09, .36†	1,5,9	12,13,14
Egg production (eggs)	-.93*[c], -.30*[d], -1.00**[e], -1.4	-.15†[g], -.17[g]	1.5,8,9	12,13
Egg production rate (%)	-.14†[a], -.06†[b], -.43††, -.23	-.35†, -.34**, -.74†	2,2,6,11	12,13,14
Fertility (%)	.11†[a], .16†[b]	-1.1†, -.44*, -.91†, -.60	2,2	12,13,14,15
Hatchability of fertile eggs (%)	-.11[a], -.44*[b], -.10†[b], -.16†[a], -.37*	-.7†, -.56**, -1.13†, -.91	1,1,3,3,5	12,13,14,15
Mortality (%) to:				
four weeks		.51, .63**		13,15
five weeks		.2†[a], .4†[b]		12,12
eight weeks	.27†[a], .26†[b], .33††		3,3,7	
housing	.15††		7	
housing to July 1	.21††		7	

Table 1. - Continued

Trait	Specie		Reference[h]	
	Domesticated chicken	Japanese quail	Chicken	Quail
Body weight (g) at: six weeks		-.2(♂♂)†, -.4(♀♀)†		12,12
eight weeks	-1.32††		10	
12 weeks	-3.68††		4	
16 weeks		-.12(♂♂), -.09(♀♀)		13
sexual maturity	-1.04		5	
4,8,12,16,20 weeks and sexual maturity		-.30(♂♂)†, -.42(♀♀)†		14,14
32 weeks	-2.04*		11	
43 weeks	-.00		1	
Egg weight (g)	-.00, -.02, -.06	-.01, -.00†	1,5,11	13,14

* ($P \leq 0.05$)

** ($P \leq 0.01$)

† Test of significance not indicated

†† Significant but level of significance not indicated

Table 1. - Continued

[a] Regression on inbreeding of dam

[b] Regression on inbreeding of offsping

[c] Mean family egg production to 300 days

[d] Survivor egg production during first six months

[e] Mean family hen-housed egg production from 1st egg to October 1st

[f] 72 week hen-housed egg production

[g] Individual egg production to 16 weeks

[h] References coded as follows:

1. Shoffner (1948)
2. Wilson (1948a)
3. Wilson (1948b)
4. Glazener et al. (1951)
5. Blow and Glazener (1953)
6. Stephenson et al. (1953)
7. MacLaury and Nordskog (1956)
8. Tebb (1957)
9. Morris (1962)
10. MacLaury and Johnson (1971)
11. Nordskog et al. (1974)
12. Sittmann et al. (1966)
13. Shinjo et al. (1971)
14. Kawahara (1972)
15. Shinjo et al. (1972)

preventing an increase in age at sexual maturity despite increasing inbreeding (Hays, 1929; Waters, 1945; Knox, 1946). However, Hays (1934) was unable to prevent an increase in this trait by selection for it.

Egg production in the chicken was shown to decrease in response to increased inbreeding (Cole and Halpin, 1922; Dunn, 1923; Goodale, 1927; Jull, 1933; Hays, 1934; Hays, 1935; Shoffner, 1948; Wilson, 1948a; Hays and Talmadge, 1949; Duzgunes, 1950; Blow and Glazener, 1953; Stephenson et al., 1953; Tebb, 1957; Crittenden and Bohren, 1962; Morris, 1962; Morgan and Kohlmeyer, 1963; Nordskog et al., 1974). Depression of egg production over time with inbreeding can usually be overcome by selection for this trait (Hays, 1924; Waters and Lambert, 1936; Knox, 1946; Schultz, 1953; Tebb, 1958; Yamada et al., 1958; Morris, 1962; Nordskog et al., 1974). Hays (1929), however, observed a decline in egg production over time despite selection.

Reduction in percent fertility with increased inbreeding has been reported by several authors (Hays, 1924; Hays, 1929; Bernier et al., 1951). Wilson (1948a), however, reported increases in fertility per one percent increase in inbreeding of the offspring and dam. Selection for traits related to fertility has usually been successful in opposing the depression of this character over time due to inbreeding (Jull, 1933; Waters and Lambert, 1936; Wilson, 1948a). On the other hand, selection for greater fecundity did not prevent a decrease in fertility over time in an inbred population of Rhode Island Reds (Knox, 1946).

Hatchability of total and/or fertile eggs has been shown to decrease with increased inbreeding (Cole and Halpin, 1922; Dunn, 1923; Hays, 1924; Jull, 1929b; Warren, 1934; Shoffner, 1948; Wilson, 1948b; Duzgunes, 1950; Blow and Glazener, 1953; Crittenden and Bohren, 1962; Morris, 1962). Jull (1929b) and Bernier et al. (1951) found the greatest effect of inbreeding on this trait when F was between 0.0 and 12.5 percent. In most inbreeding experiments, hatchability of total and fertile eggs decreased over time with increased inbreeding regardless of selection for this trait (Hays, 1929; Jull, 1933; Hays, 1934; Waters, 1945; Knox, 1946). Waters and Lambert (1936), however, were able to maintain hatchability by selection for this trait in one population of White Leghorns inbred up to 83 percent.

Early mortality, measured over periods ranging from 17 days to four weeks of age, has been shown by some authors to increase with respect to increasing levels of inbreeding (Dunn, 1923; Jull, 1929a; Byerly et al., 1934; MacLaury and Nordskog, 1956). On the other hand, Jull (1933) and Morris (1962) described inbreeding experiments in which mortality to four weeks and 25 days of age, respectively, did not increase as inbreeding increased. Several authors found that mortality among older birds increased as inbreeding increased (Hays, 1935; Waters and Lambert, 1936; Wilson, 1948b; Hays and Talmadge, 1949; MacLaury and Nordskog, 1956; Lowe and Wilson, 1965).

Body weight in the chicken appears to be either unaffected or slightly depressed by increases in inbreeding. Hays (1924) and Goodale (1927) found that body weight at first egg

did not change as inbreeding increased, while Hays (1935) reported a significant increase in weight among the progeny of inbred males over those of non-inbred males. Body weight did not change with increased inbreeding in experiments by Waters and Lambert (1936) and Shoffner (1948). Several authors reported, however, slight, but usually significant, decreases in body weight with increased inbreeding (Glazener et al., 1951; Blow and Glazener, 1953; MacLaury and Johnson, 1971; Nordskog et al., 1974). Glazener et al. (1951), Waters (1951) and Nordskog et al. (1974) showed that selection improved 12 week, 10 month and 20 week body weight over time despite increasing inbreeding. Hays (1929) maintained body weight at first egg by selection for this trait in a population of inbred Rhode Island Reds. Full-sibbing White Leghorns for three generations resulted in slower growth to three weeks of age (Dunn, 1923). Decreases in mean blastoderm size and number of somites after 38 hours of incubation (Bernier et al., 1951) and in embryo weight after two weeks of incubation (McNary et al., 1960) with increased inbreeding have been reported. In addition, Dunn (1928) found that individual and total bone length decreased as inbreeding increased in White Leghorns.

Inbreeding appears to have little effect on egg weight in the chicken. Dunn (1923) and Waters and Lambert (1936) reported both increases and decreases in average egg weight with increased inbreeding in several lines of White Leghorns. Lines of Rhode Island Reds inbred for up to five years showed no decrease in egg weight (Knox, 1946; Hays and Talmadge, 1949).

Small, usually non-significant, decreases in egg weight with inbreeding were reported by several authors (Waters, 1941; Shoffner, 1948; Blow and Glazener, 1953; Schultz, 1953; Nordskog et al., 1974). Hays (1935), on the other hand, found that the progeny of inbred Rhode Island Red males mated to Rhode Island Red females had significantly ($P \leq 0.05$) higher mean egg weights than did progeny of non-inbred males mated to females of the same breed. Selection has been successful in increasing mean egg weight despite slight inbreeding depression of this trait (Hays, 1934; Schultz, 1953; Nordskog et al., 1974).

Effects of Inbreeding on Various Traits in Domesticated Japanese Quail

Table 1 gives a comparison of linear regression coefficients for the regressions of various trait values on inbreeding between domesticated chickens and Japanese quail. Changes in trait values of approximately the same magnitude per percent increase in inbreeding exist between these two species for age at sexual maturity, egg production rate and egg weight. Mortality and hatchability increase and decrease at greater rates, respectively, per percent increase in inbreeding in quail than in chickens. Total egg production and body weight decrease at slower rates in quail than in chickens as inbreeding increases. The literature contains several examples of decreases in fertility with inbreeding in both quail and chickens although the only regression coefficients found by this author for chickens were positive.

Sittmann et al. (1966) and Shinjo et al. (1971) working with populations of quail inbred by full-sib matings for five and four generations, respectively, found that age at sexual maturity of the female quail increased with inbreeding. Kawahara (1972) reported an increase in age at sexual maturity in quail also reproduced by consecutive full-sib matings.

Sittmann et al. (1966) and Shinjo et al. (1971) found decreases in egg production to sixteen weeks of age with inbreeding for up to five generations of full-sib matings. Kulenkamp et al. (1973) expressed the responses of a variety of traits to inbreeding as deviations of the weighted trait means of a number of inbred lines from the mean of a "non-inbred" line. A deviation of -.02 of an egg per percent increase in inbreeding was reported for total egg production to 21 weeks of age. The relationship between total egg production and inbreeding was non-linear in this experiment. Sittmann et al. (1966) observed a decrease in rate of egg production between 12 and 16 weeks of age with inbreeding. A decrease in egg production rate to 60 days after first egg was reported by Kawahara (1972). Shinjo et al. (1972) found a decrease in hen-day egg production.

Fertility in quail was observed to decrease with inbreeding (Sittmann et al., 1966; Shinjo et al., 1971; Kawahara, 1972; Shinjo et al., 1972). Boesiger (1969) reported decreases in fertility relative to a control line of 33.4, 36.7 and 39.2 percent for three inbred lines after one generation of full-sib matings. In the F_3, however, fertility remained constant in two of the inbred lines while increasing in the third. Boesiger

(1969) also noted that duration of fertility after removal of the male was shorter among inbred females than among control line females. A deviation of -.08 of a percent in fertility per percent increase in inbreeding from a control line was reported by Kulenkamp et al. (1973). The relationship between fertility and inbreeding was non-linear. Some of the decreases in fertility with increased inbreeding may be due to decreases in sexual vigor (Lucotte, 1974) or to the length of storage of fertile eggs prior to incubation (Sittmann et al., 1966; Boesiger, 1969).

Decreases in hatchability of fertile eggs with inbreeding have been reported by several authors (Sittmann et al., 1966; Shinjo et al., 1971; Kawahara, 1972; Shinjo et al., 1972). Similarly, Boesiger (1969) found that hatchability of fertile eggs decreased 37.7 and 47.1 percent relative to that of a control line in two lines full-sib mated for two generations ($F = 0.375$). A deviation in percent hatchability of fertile eggs per percent increase in inbreeding from a control line of -.26 was reported by Kulenkamp et al. (1973). Peaks in mortality among those eggs not hatching occurred between one and eight days (Sittmann et al., 1966), between one and five and between 13 and 17 days (Shinjo et al., 1971, 1972) and between one and five and between 11 and 15 days (Boesiger, 1969). Lucotte (1974) showed that percentage of abnormal embryo orientations after 50 hours of incubation and frequencies of various abnormal embryo positions in eggs not hatching increased as the degree of inbreeding increased. In addition, mean embryo weights at six and 12 days

of incubation decreased with increased inbreeding (Boesiger, 1969). This decrease in embryo weight was believed to be partially responsible for the decrease in hatchability of fertile eggs due to inbreeding.

Increases in quail mortality with inbreeding were reported for mortality to four, five and 20 weeks of age (Sittmann et al., 1966; Shinjo et al., 1971; Kawahara, 1972; Shinjo et al., 1972). Boesiger (1969) compared percent mortalities for the first, second and third weeks after hatching for three consecutive generations of full-sib matings and noted the greatest increases in mortality after the first generation and during the first week after hatching. Mortality to three and seven weeks were shown by Kulenkamp et al. (1973) to increase .26 percent per percent increase in inbreeding relative to his control line. A linear relationship existed between mortality to three weeks and inbreeding.

Six week body weight in quail was observed to decrease in males and, to a greater degree, in females with inbreeding (Sittmann et al., 1966; Kawahara, 1972). This effect was attributed to a delay in sexual maturity of the females due to inbreeding. Boesiger (1969) found that eight week body weight was reduced by seven grams in males and 11 grams in females after one generation of full-sib matings. On the other hand, Shinjo et al. (1971) reported a greater decrease in 16 week body weight among males than among females as inbreeding increased. Kulenkamp et al. (1973) found a deviation from his control line

per percent increase in inbreeding of -.06 grams for three week body weight, and a deviation of -.12 grams for females and -.06 grams for males for seven week body weight. The relationship between body weight at three and seven weeks and inbreeding was non-linear.

Egg weight decreased very slightly with inbreeding (Sittmann et al., 1966; Boesiger, 1969; Shinjo et al., 1971; Kawahara, 1972). One generation of full-sib matings usually resulted in decreases in egg weight of nearly one gram. Kulenkamp et al. (1973) reported an increase in egg weight per percent increase in inbreeding of .040 grams relative to his control line.

OBJECTIVES

1. To compare calculated rates and magnitudes of inbreeding in two lines of Japanese quail under random mating *per se* and in two lines under family selection for three week body weight.
2. To compare calculated rates and magnitudes of inbreeding estimated by the variance-covariance method with theoretical values estimated from effective population size.
3. To study variation in inbreeding coefficients and shape of frequency distributions of inbreeding coefficients over time for selected and control lines of quail.
4. To estimate the effects of relatively low rates of inbreeding on a variety of fitness and economic traits in the quail over a relatively large number of generations.

EXPERIMENTAL MATERIALS AND METHODS

Stock

The quail selection experiment is being conducted primarily to determine the rate and limit of response to upward family selection for three week body weight in Japanese quail. Stock was originally obtained from the New Hampshire Fish and Game Department which maintained a large, essentially random mating population. The foundation stock for this experiment consisted of the progeny of a flock mating of 15 male and 65 female quail. Birds from the foundation stock were randomly assigned to one of four lines numbered 1 through 4.

Family Selection for Three Week Body Weight

Family selection for three week body weight was practiced in two lines designated as 1 and 4. Within each line and generation, families were ranked according to a family index. The index was based upon mean hatch and sex corrected three week body weight weighted according to the number of individuals in a family and the repeatability of three week body weight within families for that line and generation (Falconer, 1960). Individuals were ordered by wing band number within a family. Fifty pair-matings were made per generation when birds were approximately six weeks of age. The first 50 males and 50 females from families with the highest mean body weight were used as breeders. The next 15 males and 15 females were used as spares. Breeders

were mated in pairs at random except that full-sib matings were avoided. If a breeder died, it was replaced by the top ranking spare of the appropriate sex.

Selection for three week body weight was discontinued in lines 1 and 4 in generations 27 (G_{27}) and 29 (G_{29}), respectively, in an attempt to improve declining reproductive performance in these lines. The mating system within these lines was the same as that within the control lines (described below) from these generations through G_{38}.

Reproducing the Control Lines

The remaining two lines, designated 2 and 3 served as control lines. Fifty pair-matings were made at random with the exception of the avoidance of full-sib matings within each line each generation. Within a line, one male and one female breeder were chosen at random per family whenever possible. If not, more than one male or female was chosen from some families. In each line, 15 male and 15 female spares were taken from pens chosen at random. Dead breeders were replaced by spares taken at random from all spares of that sex for that line and generation.

Traits Measured

Individual observations on a variety of economic and fitness traits, in addition to the trait under selection, were made within all lines. Traits for which values were recorded on electronic data processing cards were studied with regard to their response to inbreeding and included:

1. Egg production (EP): The total number of eggs layed

by a hen during 11 five-day weeks to 119 days

2. Fertility (FE): The percentage of the total number of eggs set for a hen which were fertile as determined by candling and breaking eggs which appeared infertile on the seventh day and breaking all unhatched eggs on the 18^{th} day of incubation
3. Hatchability of fertile eggs (HFE): The percentage of the total number of fertile eggs for a hen which hatched during the 18-day incubation period
4. Hatchability of total eggs (HTE): The percentage of the total number of eggs set for a hen which hatched during the 18-day incubation period
5. Family size (FS): The total number of chicks hatched from all eggs set for both the first and second hatch
6. Three week body weight (TW): The weight in grams of a quail on day 21 post-hatching corrected within generation for the effects of hatch and sex
7. Adult body weight (AW): The weight, in grams, of an adult male weighed at 15½ weeks of age or of an adult female weighed at 17½ weeks of age corrected for the effect of hatch
8. Mean egg weight (EW): The mean weight, in grams, of all eggs layed by a hen during two five-day weeks (10 days) when the quail were between 15½ and 17½ weeks of age

Management

Selected and control lines of chicks were brooded together in five deck batteries, each deck containing up to 40 chicks from G_1 through G_{12}. Chicks from the two selected lines were randomized to decks of brooding batteries such that both lines were brooded intermingled on the same decks beginning in G_{13}. Control lines were handled similarly. Beginning in G_{26} each line was randomized separately to decks in the brooding batteries. Room temperature in the brooder room was thermostatically controlled by a circulating hot water system and by an exhaust fan, and deck temperatures by individual adjustable electric heating units. Chicks were fed a commercially mixed turkey starter feed throughout except that the protein level was raised from 24 to 31 percent in G_9.

Quail chosen as breeders were randomized according to line to individual pair mating pens within batteries located in a separate adult quail room. Room temperature was thermostatically controlled as in the brooder room except that individual batteries had no heaters. Adult quail were fed a commercially mixed feed containing approximately 24 percent protein, 1.90 percent calcium and 0.80 percent total phosphorus from G_1 through G_{11}. From G_{11} through G_{38} they were fed a custom mixed feed containing approximately 29 percent protein, 3.00 percent calcium and 0.90 percent total phosphorus.

Calculation of Wright's Coefficient of Inbreeding

The variance-covariance method of calculating inbreeding

coefficients devised by Lush and co-workers and illustrated by Rice *et al.* (1970) was used in this study. This method is based on the fact that the value of Wright's coefficient of inbreeding for an individual is equal to the covariance of an individual with himself minus 1.0. Covariances of individuals with themselves are, in turn, determined from covariances between different individuals. These covariances are calculated as follows:

1. The covariance of an individual with himself, or his variance, is equal to one-half the covariance of his sire with his dam (i.e., his coefficient of inbreeding) plus 1.0
2. The covariance between two individuals is equal to one-half the sum of the covariance of one of the individuals with first the sire and then the dam of the other individual

Covariances between sires and dams make up the numerator in the formula for the coefficient of relationship. Covariances between all individuals within a generation and between those in consecutive generations provide, therefore, all the information necessary to calculate both inbreeding and relationship coefficients.

In practice, coefficients of inbreeding are calculated for two generations first by writing the variances and covariances between all individuals in the base generation, second by calculating the covariances of all individuals in the base generation with those in the next generation, and third by determing

variances and covariances among individuals in the next generation. Therefore, coefficients of inbreeding are calculated each generation from covariances in the previous generation. Variances and covariances are normally arranged in tabular form with variances for individuals displayed along a diagonal of the table. This method is illustrated in Figure 1 on page 35.

The variance-covariance method of calculating inbreeding coefficients was programmed in Fortran IV on an IBM 360-50 computer. The level of inbreeding was assumed to be zero in the base generation of each line. Program output for lines 1 through 4 from G_1 through G_{36} included coefficients of inbreeding for all individuals together with histograms of these coefficients. In addition, the following ten statistics were given for (1) the coefficients of inbreeding of all individuals, (2) of breeders only, and (3) of families only:

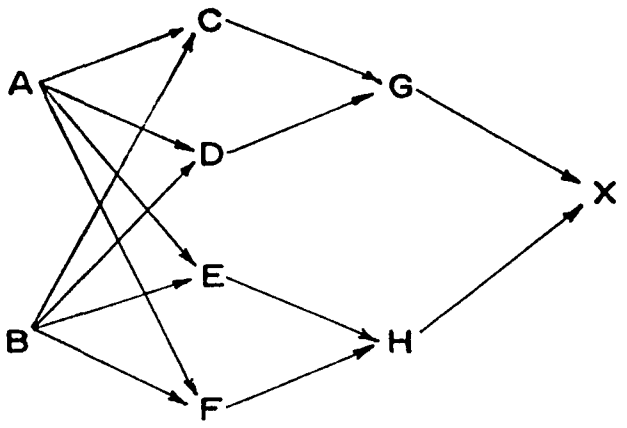
1. Mean
2. Median
3. Variance
4. Standard deviation
5. Minimum value
6. Maximum value
7. Range
8. Standard error of the mean
9. Coefficient of skewness
10. Value of Geary's a (measure of kurtosis)

Computer output was checked for accuracy by comparison with results of hand calculations for some hypothetical pedigree data.

Regression Analyses

A computer program was written to calculate within line and generation the linear and quadratic regressions, for each trait separately, of trait (Y) on individual inbreeding coefficient (X) for G_5 through G_{36}. Another program was written to calculate a single linear regression coefficient for each line and trait based upon the within-generation corrected sums of squares ($\Sigma x^2, \Sigma y^2$) and corrected crossproducts (Σxy) pooled over the 32 generations. Linear regression coefficients were tested for significance using the null hypothesis that a regression coefficient was equal to zero. The 0.05 probability level was used for testing the significance of a linear regression coefficient and of the improvement of a quadratic over a linear model. This probability level was also used for all other tests in this manuscript.

PEDIGREE OF INDIVIDUAL X



VARIANCE - COVARIANCE TABLE

		G_1		G_2				G_3		G_4
	SIRE			A	A	A	A	C	E	G
	DAM			B	B	B	B	D	F	H
	INDIVIDUAL	A	B	C	D	E	F	G	H	X
G_1	A	1.0	0	.5	.5	.5	.5			
	B		1.0	.5	.5	.5	.5			
G_2	C			1.0	.5	.5	.5	.75	.5	
	D				1.0	.5	.5	.75	.5	
	E					1.0	.5	.5	.75	
	F						1.0	.5	.75	
G_3	G							1.25	.5	.875
	H								1.25	.875
G_4	X									1.25

FIGURE I. CALCULATING COEFFICIENTS OF INBREEDING BY THE VARIANCE - COVARIANCE METHOD

RESULTS AND DISCUSSION

Magnitude and Rate of Inbreeding in Control and Selected Lines

Individual, Breeder and Family Inbreeding Coefficients

Histograms of inbreeding coefficients together with values for the ten statistics listed in the previous section were obtained for breeders and families as well as all individuals each line each generation. Separate regression lines for the linear regressions of individual and breeder mean percent inbreeding on generation number were calculated for each selected line over the selection period and for each control line over all generations. The difference between breeder and individual inbreeding was tested for significance by (1) comparing these regression lines using the method of Snedecor and Cochran (1967) for control and selected lines, and by (2) applying Wilcoxon's signed rank test (Steel and Torrie, 1960) to pairs of mean percent inbreeding values in the selected lines for the selection period. Residual variances, slopes and elevations of the two regression lines never differed significantly, i.e., the magnitudes and rates of inbreeding among breeders were not, according to regression line comparisons, significantly different from those for all individuals. Wilcoxon's test, however, showed that breeders were significantly less inbred, on the average, than the average inbreeding of all individuals from which they were chosen

in the selected lines during selection. Comparisons between regression lines must have overlooked small (maximum of 0.18 percent) yet significant differences in mean percent inbreeding between breeders and individuals in the selected lines each generation. Breeders were expected to be less inbred, on the average, than the average inbreeding of the entire population each generation since inbreeding significantly depressed three week body weight within generations in this experiment and individuals with lower degrees of inbreeding were heavier.

Family inbreeding statistics were not weighted by the number of individuals in a family. Since the number of individuals in each family was not the same, these statistics were not good indicators of the behavior of inbreeding values.

Breeder and family inbreeding histograms and statistics will not be discussed further since the family inbreeding values are relatively unimportant and the individual and breeder inbreeding coefficients were similar. The remainder of the thesis will deal, therefore, with individual inbreeding values.

Differences among Lines

Mean percent inbreeding was plotted against generation number for lines 1 through 4 for G_1 through G_{36} in Figure 2. The selected lines (1 and 4) were, on the average, 3.2 times more inbred than the average of the two control lines. Inbreeding was expected to accrue more rapidly under family selection than under random mating <u>per se</u> (Falconer, 1960). Differences in the degree of inbreeding also existed <u>between</u> selected lines and <u>between</u> control lines. Line 2 was 1.05 times as inbred as line 3.

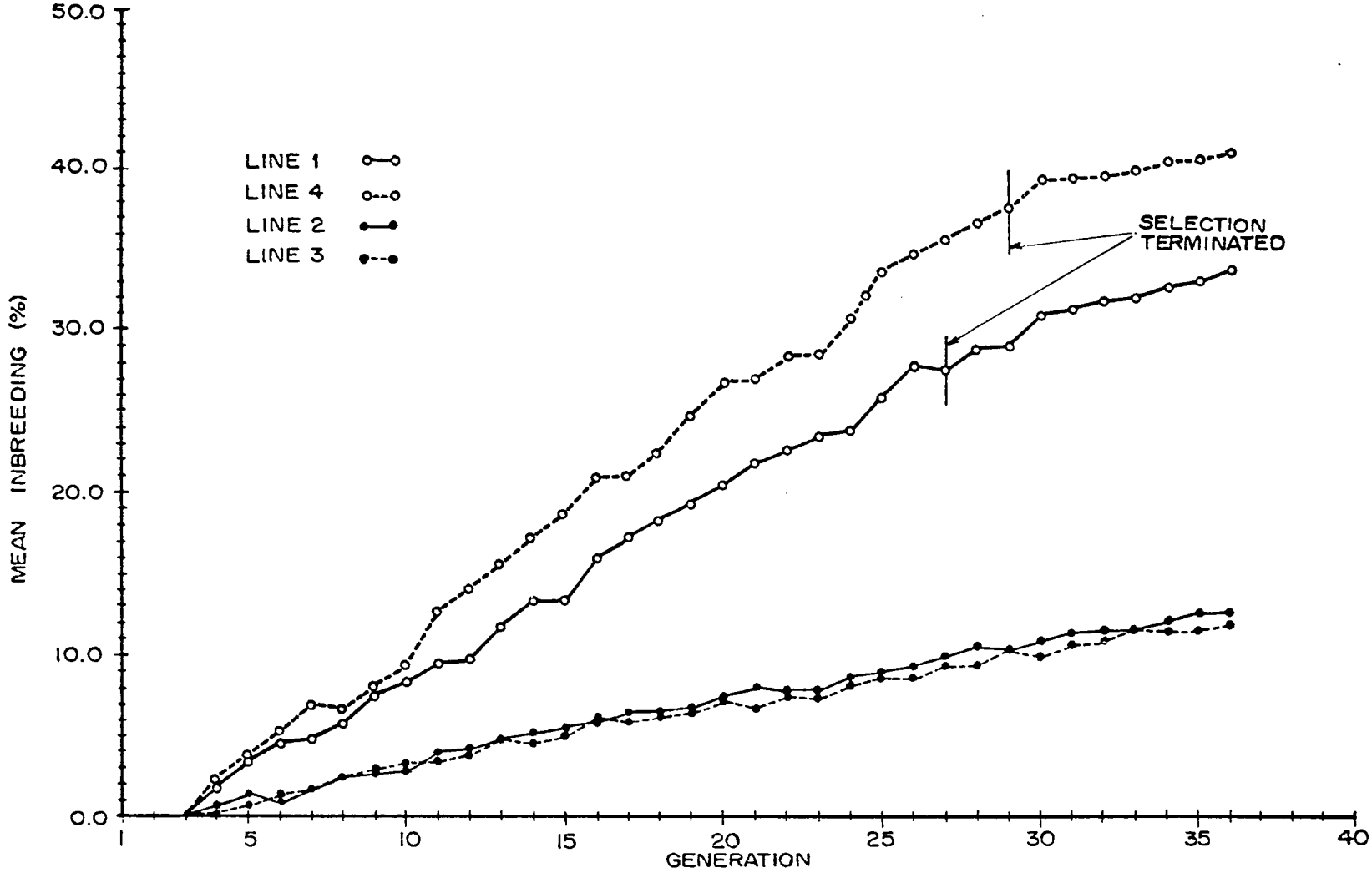


FIGURE 2. MEAN PERCENT INBREEDING OF INDIVIDUALS IN LINES 1 THROUGH 4, GENERATIONS 1 THROUGH 36

Line 4 was 1.25 times as inbred as line 1 but mean percent inbreeding in these lines remained generally similar until G_{11}. Interestingly enough, response to family selection for three week body weight was greater in line 4 than in line 1. Jones (1969) reported that in Drosophila rates of inbreeding were generally higher in lines showing the greater response to selection.

Linear regressions of mean percent inbreeding on generation were calculated for lines 1 and 4 for the selection period and for the control lines over all generations. Comparisons of residual variances, slopes and elevations of these regression lines were made between lines 1 and 4, 2 and 3, and 1 and 2 using the method of Snedecor and Cochran (1967). Differences between residual variances of regression lines were never significant but differences between slopes and elevations were significant for all comparisons. Variation around regression lines, therefore, did not differ significantly for any comparisons but the quail lines compared differed significantly in rate and magnitude of inbreeding.

Mean percent inbreeding by five generation intervals is given in Table 2. Mean inbreeding was much greater for lines 1 and 4 than for lines 2 and 3. In G_{35}, the mean percent inbreeding was 40 and 33 percent in lines 4 and 1, respectively, compared to values of 11 and 13 percent in lines 2 and 3, respectively. The selected lines differed more in inbreeding than did the control lines.

Rate of inbreeding determined by linear regression of mean percent inbreeding on generation is presented in Table 3.

Table 2. - Calculated mean percent inbreeding at five generation intervals for lines 1 through 4

Generation	Line 1	Line 4	Line 2	Line 3
5	3.32±.15[a]	3.81±.18	1.21±.12	0.60±.07
10	8.29±.10	9.29±.18	2.80±.09	3.04±.08
15	13.31±.13	18.79±.17	5.35±.09	4.93±.09
20	20.47±.17	26.76±.15	7.33±.11	7.09±.10
25	25.83±.20	33.54±.17	8.65±.06	8.59±.10
30	30.77±.19	39.20±.17	10.85±.13	9.89±.07
35	33.03±.08	40.38±.03	12.67±.07	11.46±.07

[a]Standard error

Table 3. - Regression coefficients for the linear regression of calculated generation mean percent inbreeding on generation number for lines 1 through 4

Period	Line 1	Line 4	Line 2	Line 3
Selection (G_3-G_{27})[b]	1.16[a]	1.46	0.40†	0.38†
Post-selection (G_{28}-G_{36})[c]	0.56	0.29	0.31	0.30
All generations (G_3-G_{36})	1.06†	1.32†	0.38†	0.36†

[a] All linear regression coefficients are significant ($P \leq 0.05$) and each corresponding $r^2 > 0.91$

[b] G_3-G_{29} for line 4

[c] G_{30}-G_{36} for line 4

† Significant improvement ($P \leq 0.05$) of quadratic over linear model

All linear regression coefficients were significant and the coefficient of determination (r^2) for inbreeding and generation number was greater than 0.91 in all cases. Therefore, rate of inbreeding was significantly greater than zero and a close relationship existed between inbreeding and generation number in all lines. Rate of inbreeding was greater in line 4 than in line 1 because the mean number of breeders chosen per family was larger and the mean number of families producing breeders were smaller per generation in line 4 than in line 1. Inbreeding in line 4 increased 1.46 percent per generation during selection but only 0.29 percent per generation during relaxed selection, a difference of 1.17 percent. Inbreeding in line 1 increased 1.16 percent per generation during selection and 0.56 percent per generation during relaxed selection, a difference of 0.60 percent. In the control lines, inbreeding dropped from 0.40 to 0.31 percent per generation in line 2 and from 0.38 to 0.30 percent per generation in line 3 between the period of selection and the period of relaxed selection. This was unexpected since neither the number of breeders chosen nor the number of families producing breeders per generation changed markedly over time.

Quadratic regressions (see footnote Table 3) described the relationship between inbreeding and generation number significantly better than did linear regressions for lines 2 and 3 through G_{27} and for all lines through G_{36}, and thus reflected the reduction over time in inbreeding rates.

Estimation of Inbreeding from Effective Population Size

Comparison of calculated inbreeding coefficients (Wright's

method) with theoretical values estimated from breeding structure may serve as experimental checks on inbreeding theory and indicate the extent to which inbreeding may be reduced by avoiding full-sib matings in each line. Theoretical increases in inbreeding per generation were estimated using the inbreeding effective population number (N_I) (Crow, 1964) for each line through G_{36}. Inbreeding coefficients obtained by Wright's method will be referred to as calculated inbreeding in contrast to theoretical inbreeding based upon effective population size. The effective population number for a particular generation depended on the number of breeders (N'), the mean family size (μ_k) and the variance of family size (σ^2_k) according to the formula:

$$N_I = \frac{N'\mu_k - 1}{\mu_k - 1 + \sigma^2_k / \mu_k}$$

Change in inbreeding per generation (ΔF) was calculated using the following relationship:

$$\Delta F = \frac{1}{2N_I}$$

Theoretical mean percent inbreeding by five generation intervals and regression of theoretical inbreeding on generation number are given in Tables 4 and 5 for lines 1 through 4, respectively. Theoretical mean coefficients of inbreeding (Table 4) and theoretical rates of inbreeding (Table 5) for the control lines were very similar to the calculated values shown in Tables 2 and 3. Theoretical inbreeding rates for the selected lines estimated over all generations were, however, 0.20 and 0.28 percent greater per generation than the calculated values for lines 1 and 4, respectively. The formula for N_I does not consider the

Table 4. - Theoretical mean percent inbreeding based on effective population size at five generation intervals for lines 1 through 4

Generation	Line			
	1	4	2	3
5	6.8	7.0	1.7	1.8
10	13.1	15.1	4.0	4.1
15	19.5	24.2	6.1	6.3
20	26.6	32.9	7.8	8.0
25	34.0	42.5	9.8	9.8
30	39.2	48.6	11.9	11.7
35	42.2	51.1	13.8	13.4

Table 5. - Regression coefficients for the linear regression of theoretical generation mean percent inbreeding on generation number for lines 1 through 4

Period	Line 1	4	2	3
Selection (G_3-G_{27})[b]	1.39[a]	1.79	0.40	0.40
Post-selection (G_{28}-G_{36})[c]	0.63	0.50	0.39	0.35
All generations (G_3-G_{36})	1.26	1.60	0.40	0.38

[a] All linear regression coefficients are significant ($P \leq 0.05$)

[b] G_3-G_{29} for line 4

[c] G_{30}-G_{36} for line 4

avoidance of full-sib matings which actually was practiced in each line. Differences between theoretical and calculated inbreeding coefficients were greatest in lines where there was the greatest avoidance of full-sib matings. The average number of families from which breeders were chosen during the selection period was 21 and 18 for lines 1 and 4, respectively, compared to 43 for each control line. Since the same number of breeders were chosen normally from each line each generation, more breeders were chosen per family in the selected than in the control lines. The probability, therefore, that two mates chosen at random from all breeders for a particular line and generation would be full-sibs would be greater in the selected than in the control lines and random mating would be more restricted in the selected lines.

Distributions of Inbreeding Coefficients within Generations

A study of distributions of inbreeding coefficients appears not to have been reported. These distributions within lines and generations are described here. Histograms of inbreeding values for several generations within each line are discussed. Changes in variation of inbreeding coefficients over generation within a line were measured by calculating ranges and coefficients of variation of inbreeding values. Degrees to which distributions departed from normality were measured by calculating coefficients of skewness and kurtosis for each line each generation. This information might aid in estimating the shape of an inbreeding distribution and proportions of individuals in different inbreeding classes from known rate and magnitude of inbreeding.

Histograms of Inbreeding Coefficients

Distributions of coefficients of inbreeding by five generation intervals for each line are presented in histogram form in Figures 3 through 5. Increases in inbreeding over time were reflected in a shift of the histograms to the right in each figure. This shift was greater in lines 1 and 4 than in lines 2 and 3. Frequently the distributions were not continuous, i.e., some inbreeding classes contained no individuals. Distributions were usually positively skewed with representatives of a few highly inbred families lying far to the right of the mean. Control lines were more positively skewed than selected lines. In the selected lines, the distributions appeared to more nearly approach normality in the intermediate generations. Differences among distributions in degree of variation (measured by range and coefficient of variation) and degree of departure from normality (measured by coefficient of skewness and Geary's $\underline{a}$) were studied in detail and are discussed in the following paragraphs.

Range of Inbreeding Coefficients

Range was found by taking the difference between maximum and minimum inbreeding values within any one generation. Ranges were plotted by generation for the control lines in Figure 6 and the selected lines in Figure 7. The largest ranges and the greatest fluctuations in range were observed over the first 19 generations of line 4. This may have been due to small numbers of matings between closely related birds producing a few relatively highly inbred offspring. For example, two birds in G_5

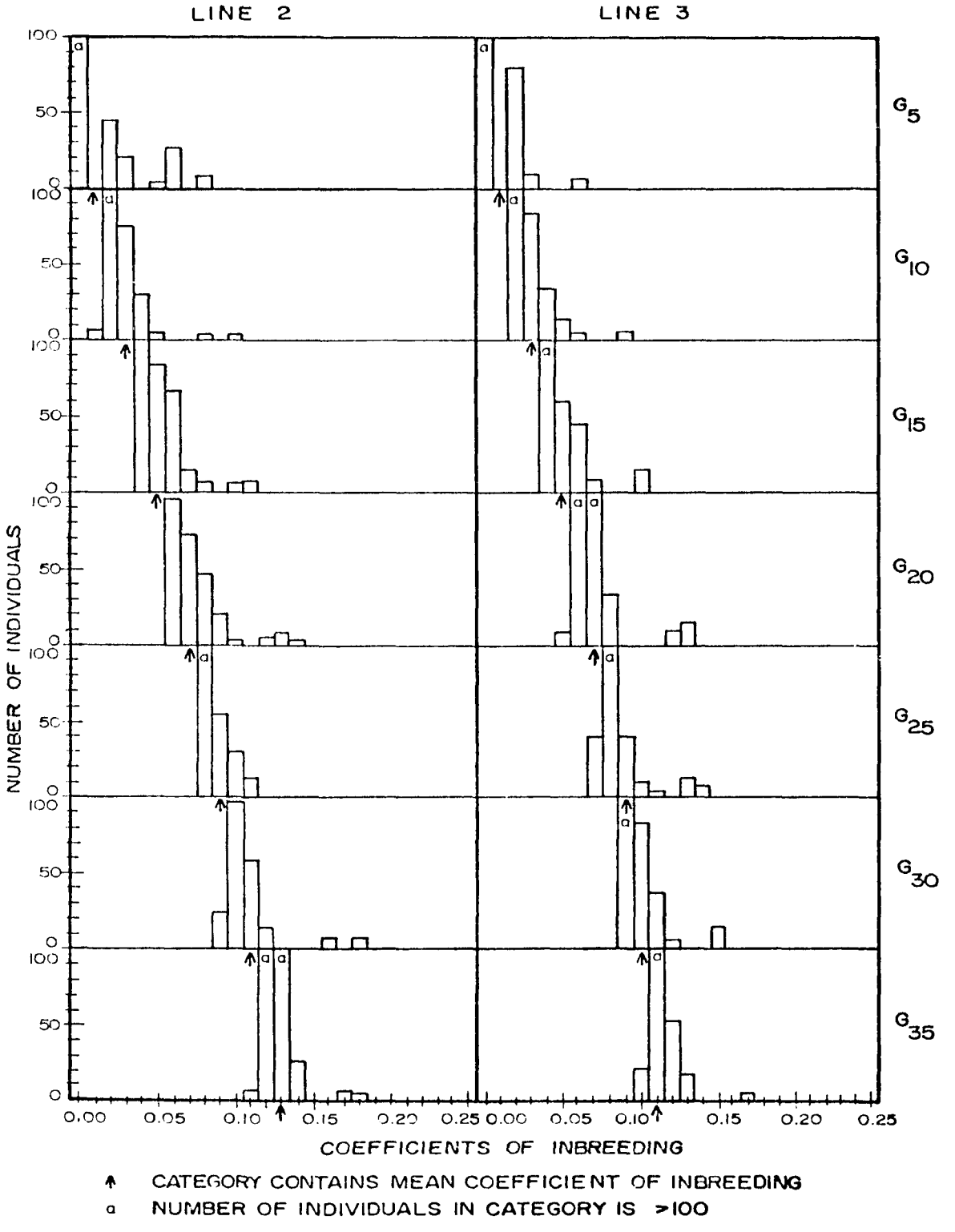


FIGURE 3. HISTOGRAMS OF COEFFICIENTS OF INBREEDING FOR LINES 2 AND 3 AT FIVE GENERATION INTERVALS

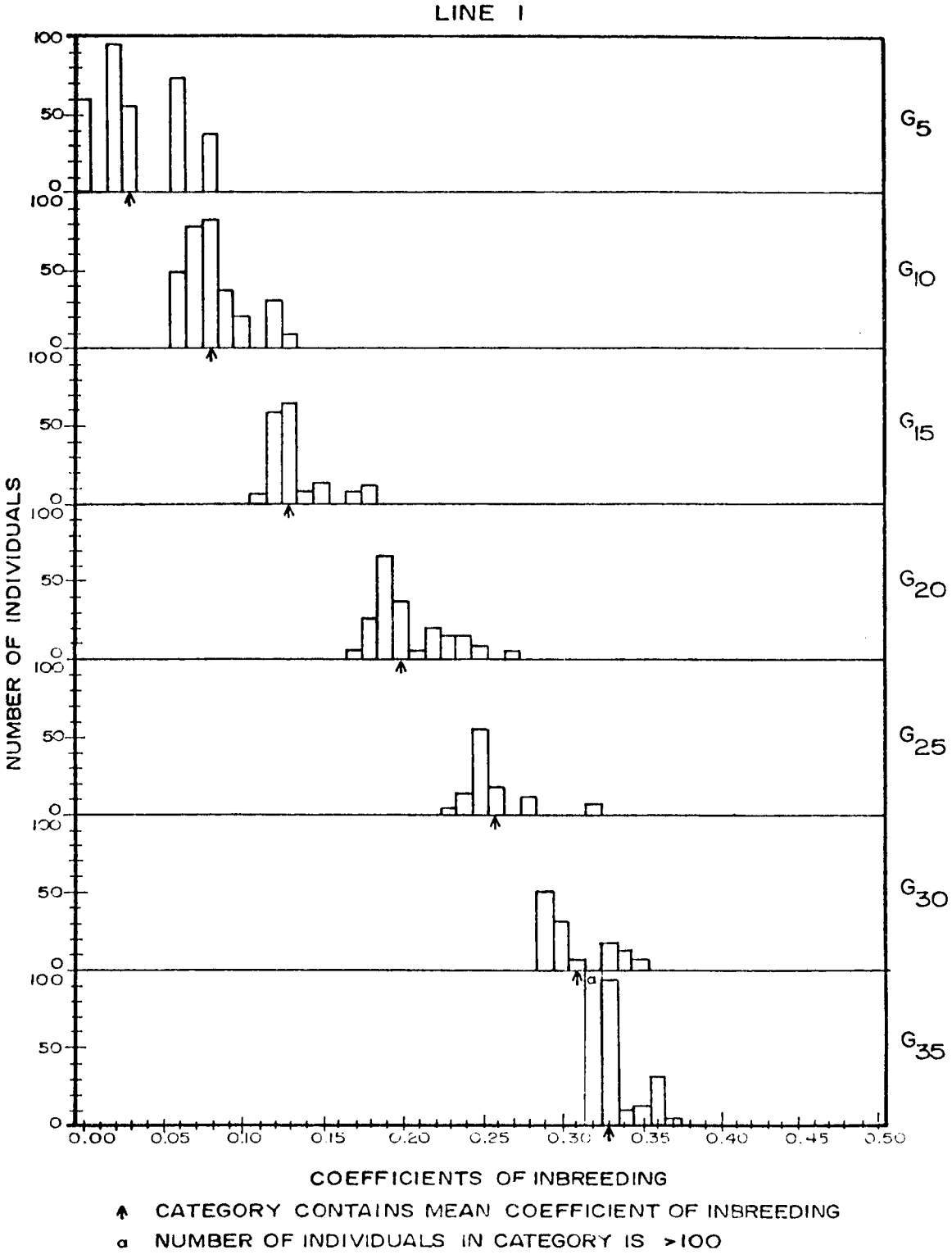


FIGURE 4. HISTOGRAMS OF COEFFICIENTS OF INBREEDING FOR LINE 1 AT FIVE GENERATION INTERVALS

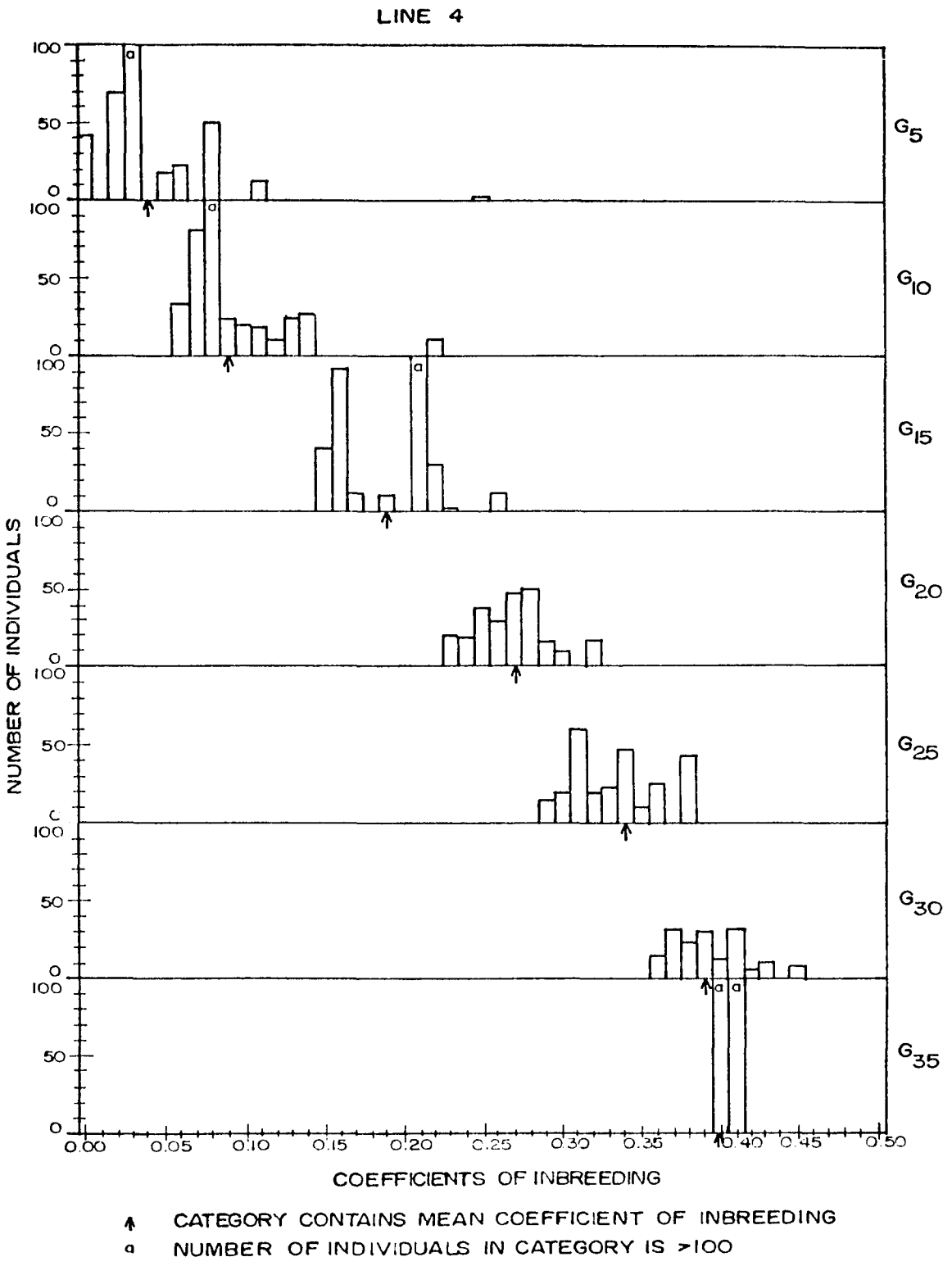


FIGURE 5. HISTOGRAMS OF COEFFICIENT OF INBREEDING FOR LINE 4 AT FIVE GENERATION INTERVALS

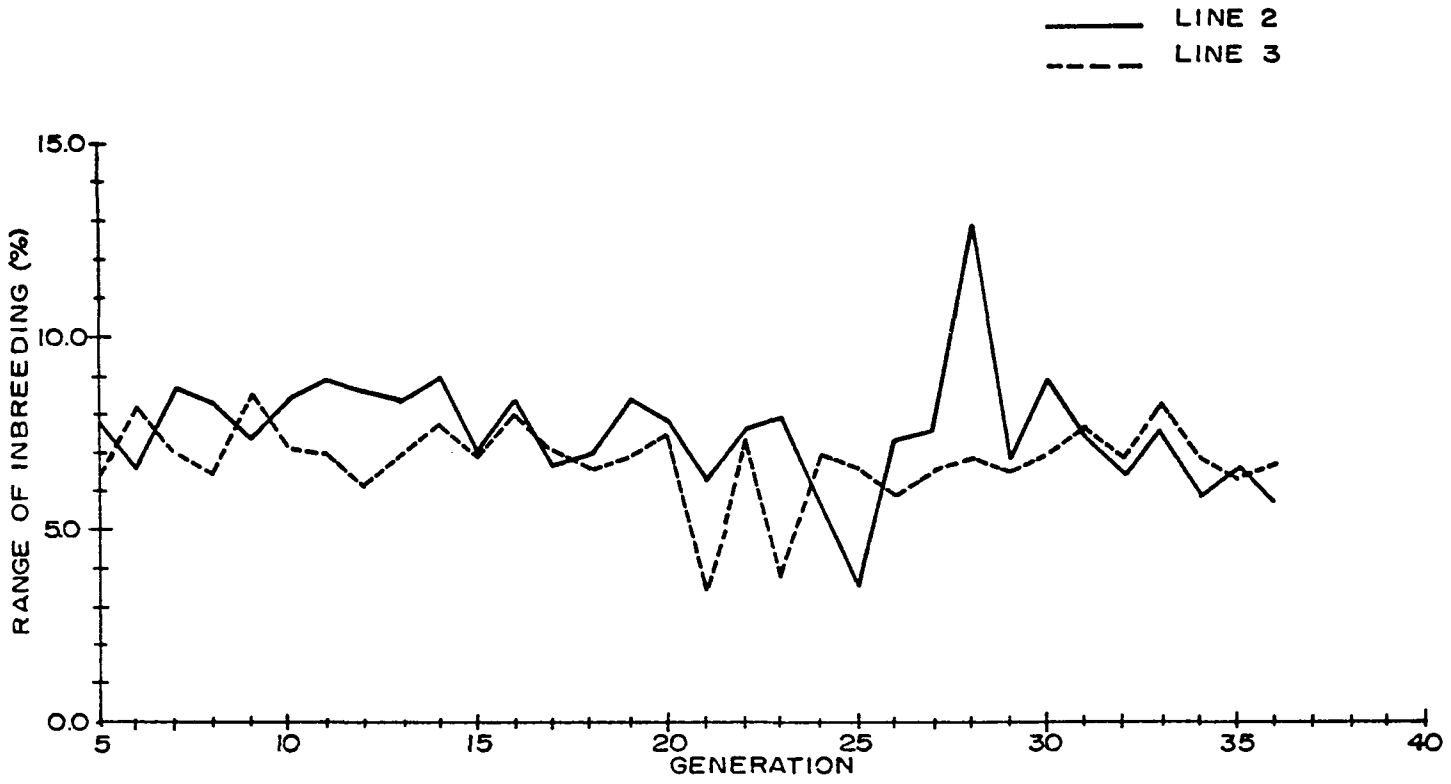


FIGURE 6. RANGE OF INBREEDING COEFFICIENTS FOR LINES 2 AND 3, GENERATIONS 5 THROUGH 36

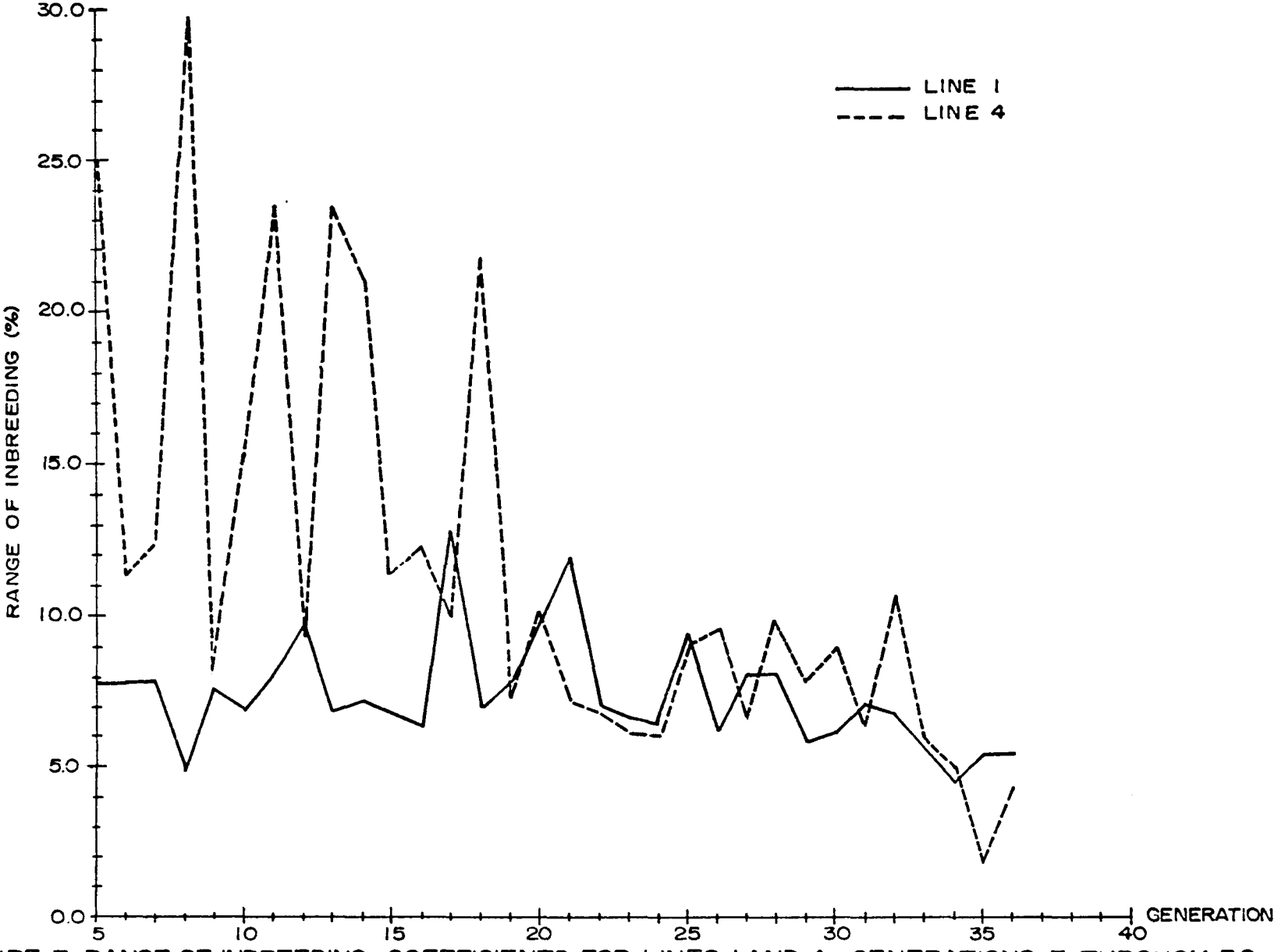


FIGURE 7. RANGE OF INBREEDING COEFFICIENTS FOR LINES 1 AND 4, GENERATIONS 5 THROUGH 36

each inbred 25 percent resulted from a single accident mating between a pair of full-sibs in G_4. Range decreased to 2.0 percent in G_{35} of line 4. This likely was due to a decrease in the number of families producing offspring from 45 in G_{33} to 31 in G_{34}. Range of inbreeding for all lines normally varied between five and 10 percent but was relatively lower in the selected lines over the last four generations.

Coefficients of Variation of Inbreeding Coefficients

This measure of variation was used in addition to the range because means and standard deviations varied between lines and over time. Coefficients of variation were calculated for each generation in the usual way. Coefficients of variation, plotted by generation, are shown for control and selected lines in Figures 8 and 9, respectively. Large initial variation in all lines was the result of small mean inbreeding coefficients (denominators in the calculation of coefficients of variation) in the early generations. Variation decreased rapidly to G_{15} and decreased almost linearly with increasing inbreeding thereafter. The initial decrease in variation was attributed to slightly greater rates of inbreeding and mean inbreeding values over the first several generations since standard deviations of inbreeding values (numerators in the calculation of coefficients of variation) showed no general decrease over time within a line. Variation among inbreeding coefficients within control lines was almost twice as great as that within selected lines. Likely this was due to breeders having been chosen from a relatively larger number of families in the control lines than in the selected lines and to the more rapid rates of inbreeding in the selected lines.

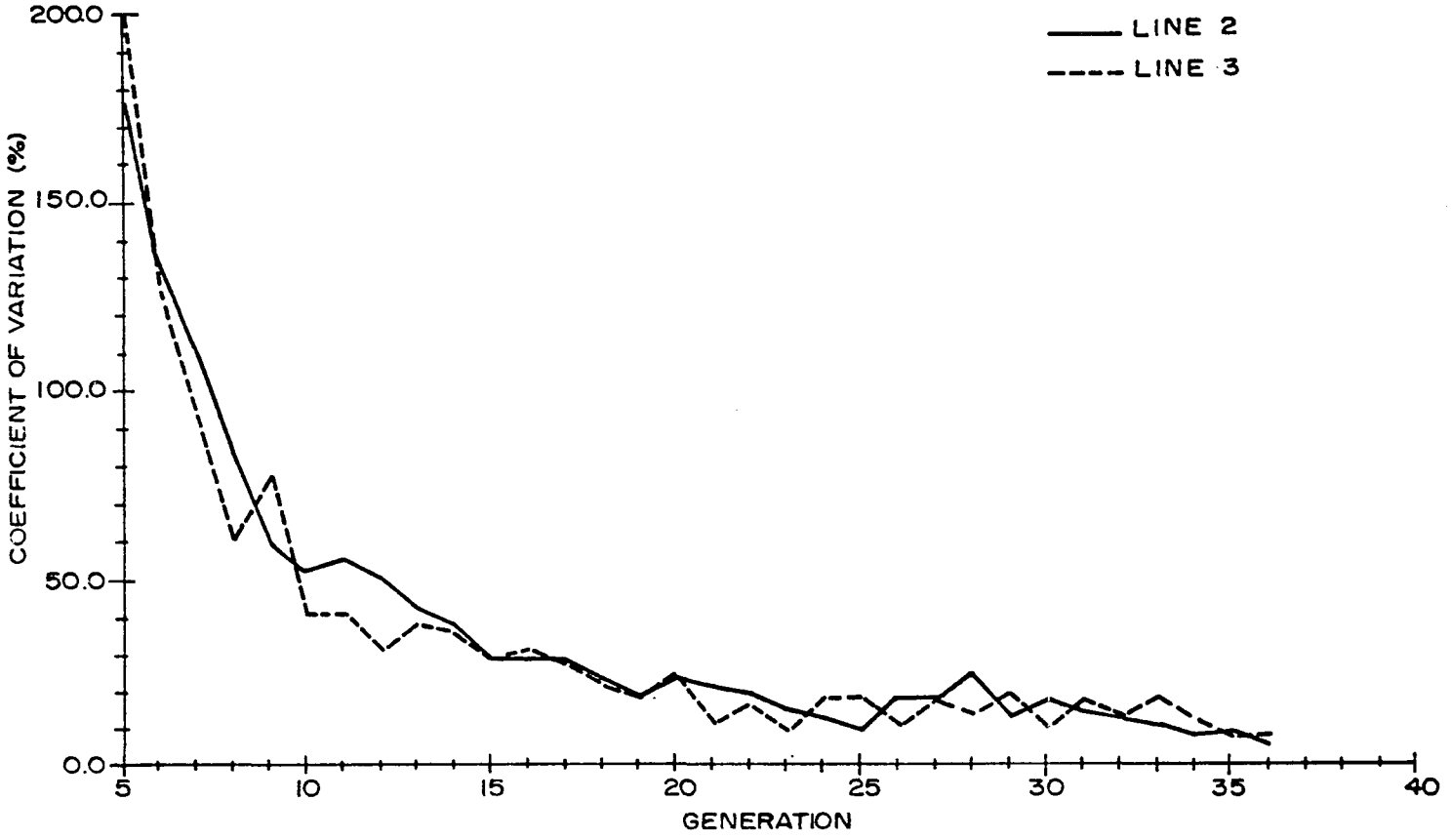


FIGURE 8. COEFFICIENTS OF VARIATION OF INBREEDING COEFFICIENTS FOR LINES 2 AND 3, GENERATIONS 5 THROUGH 36

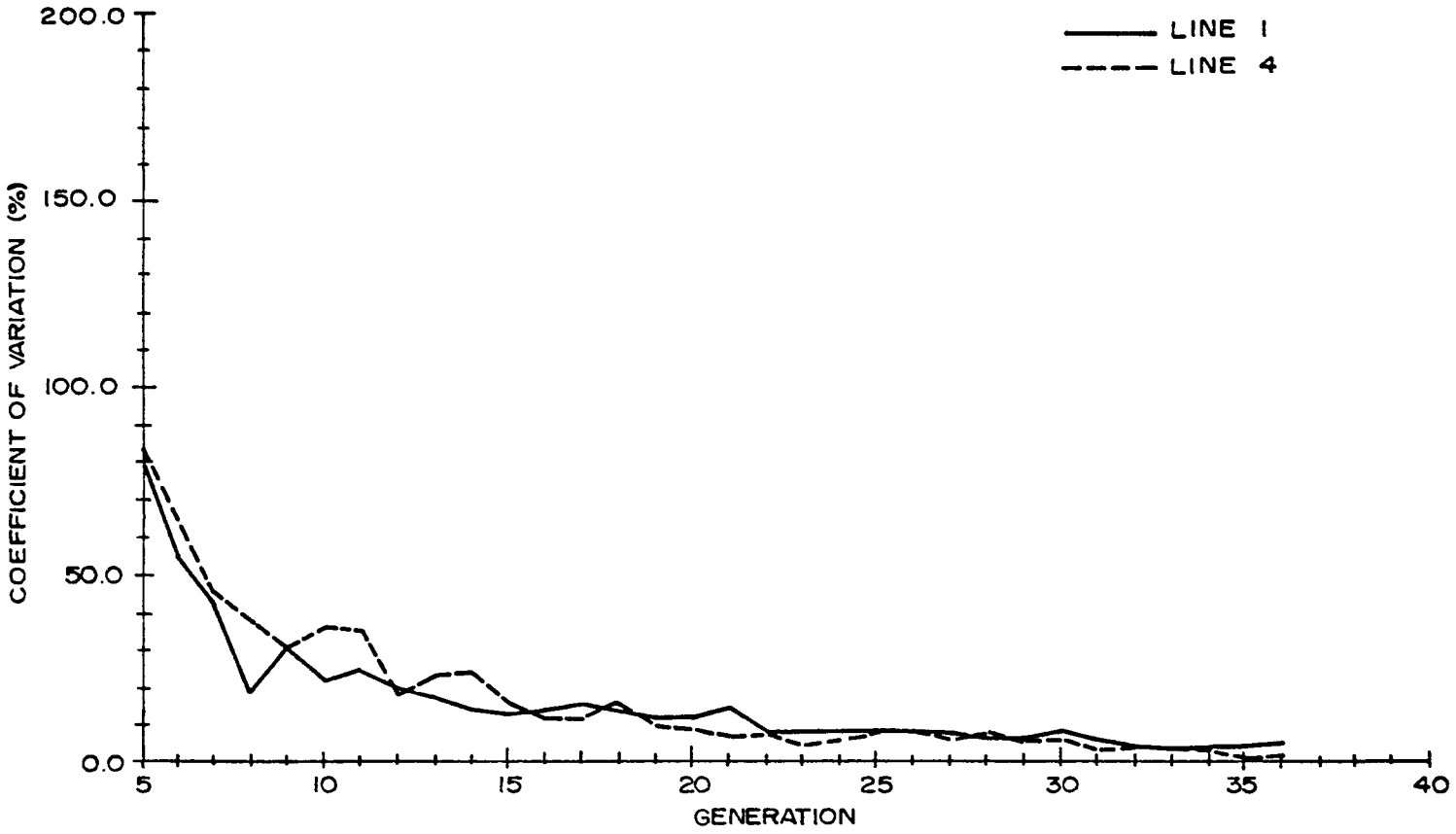


FIGURE 9. COEFFICIENTS OF VARIATION OF INBREEDING COEFFICIENTS FOR LINES 1 AND 4, GENERATIONS 5 THROUGH 36

Coefficients of Skewness

Coefficients of skewness were calculated as one test of normality for distributions of individual inbreeding coefficients for each line each generation. These coefficients were plotted against generation number for the controls (Figure 10) and for the selected lines (Figure 11). All coefficients were positive. Positive skewness implies non-normality of the distribution, i.e., low inbreeding values were grouped close to the mean while high inbreeding values formed a tail extending far above the mean. Horizontal lines drawn at coefficients of 0.25 and 0.24 were added to Figures 10 and 11, respectively. These values were taken from a table for testing skewness (Snedecor and Cochran, 1967) and were based on the average number of individuals per generation for the two control lines combined and for the two selected lines combined, respectively. All coefficients above these lines were significantly positive. Coefficients in the control lines were all significant and only four were non-significant in the selected lines. Degree of skewness was generally higher in the control lines than in the selected lines and showed no general tendency to increase or decrease over time. Skewness in the selected lines first decreased, with values between G_{16} and G_{26} occasionally indicating normality, and then increased to near their original values over the period of relaxed selection.

A Measure of Kurtosis

Geary's $\underline{a}$ was used to measure the degree of kurtosis as an additional test of normality. Peaked distributions contain

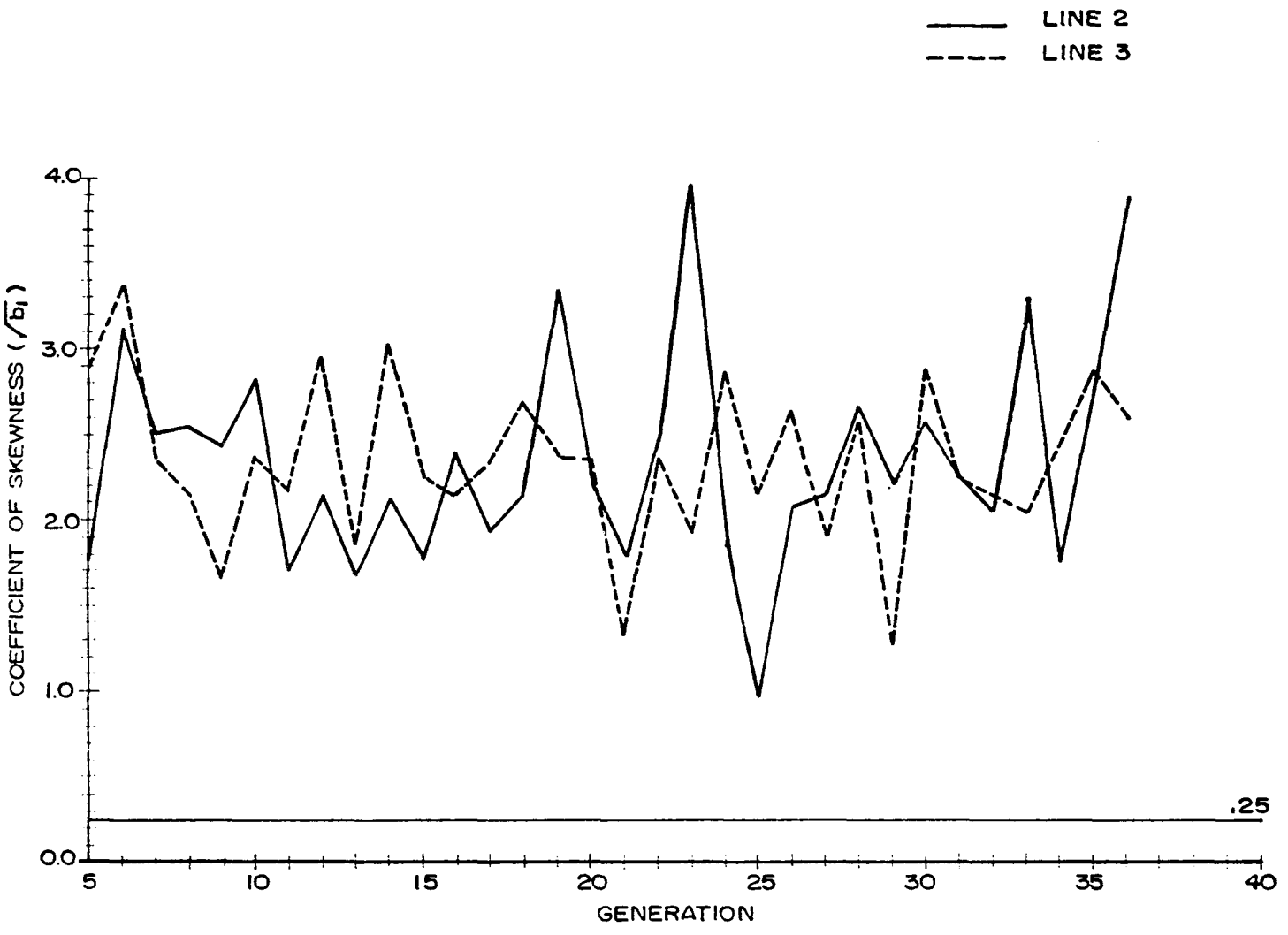


FIGURE 10. COEFFICIENTS OF SKEWNESS OF INBREEDING COEFFICIENTS FOR LINES 2 AND 3, GENERATIONS 5 THROUGH 36

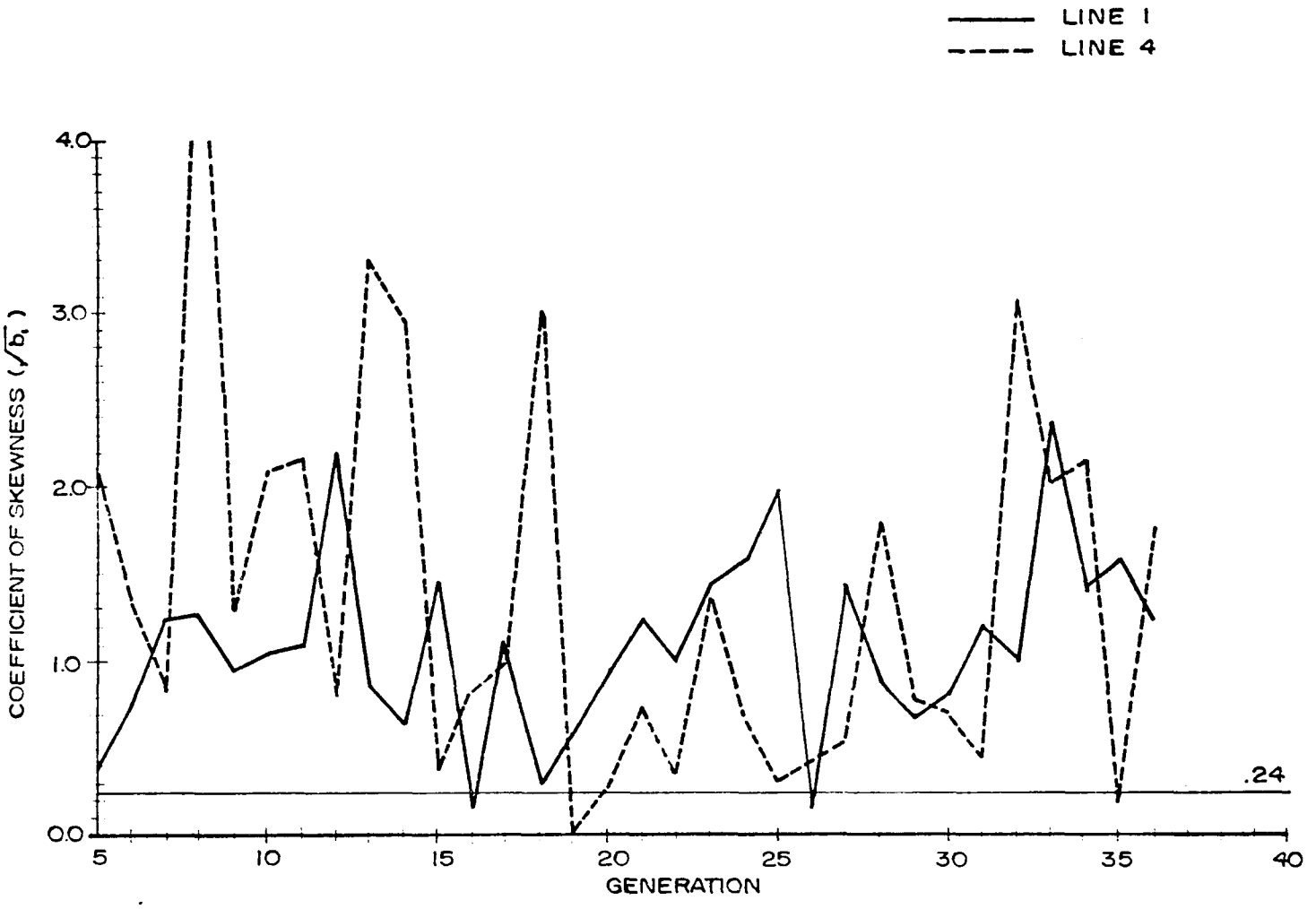


FIGURE 11. COEFFICIENTS OF SKEWNESS OF INBREEDING COEFFICIENTS FOR LINES 1 AND 4, GENERATIONS 5 THROUGH 36

inbreeding coefficients concentrated near the mean. Flattened distributions contain coefficients concentrated more in the flanks than close to or far from the mean. Values for Geary's a were plotted against generation number for control lines (Figure 12) and for selected lines (Figure 13). Three horizontal lines were drawn within each figure at values taken from a table for testing kurtosis (Snedecor and Cochran, 1967) which were based on the average number of individuals per generation for control and selected lines, separately. The middle line separated peaked distributions, for values lying above it, from flattened distributions, for values below it. Values above the upper line indicated significantly peaked distributions while those below the lower line indicated significantly flattened distributions. Almost all the distributions in the control lines were significantly flattened and none was significantly peaked. Initially, distributions within the selected lines were in general either significantly flattened, or normal, with regard to peakedness. Most became significantly peaked between G_{15} and G_{30} and significantly flattened thereafter.

General Trends in the Shape of the Distributions of Inbreeding Coefficients

Control and selected lines differed consistently in variation of inbreeding values and in distributions of inbreeding coefficients. In the control lines, range of inbreeding values remained fairly constant from generation to generation, but the coefficients of variation of inbreeding within generation

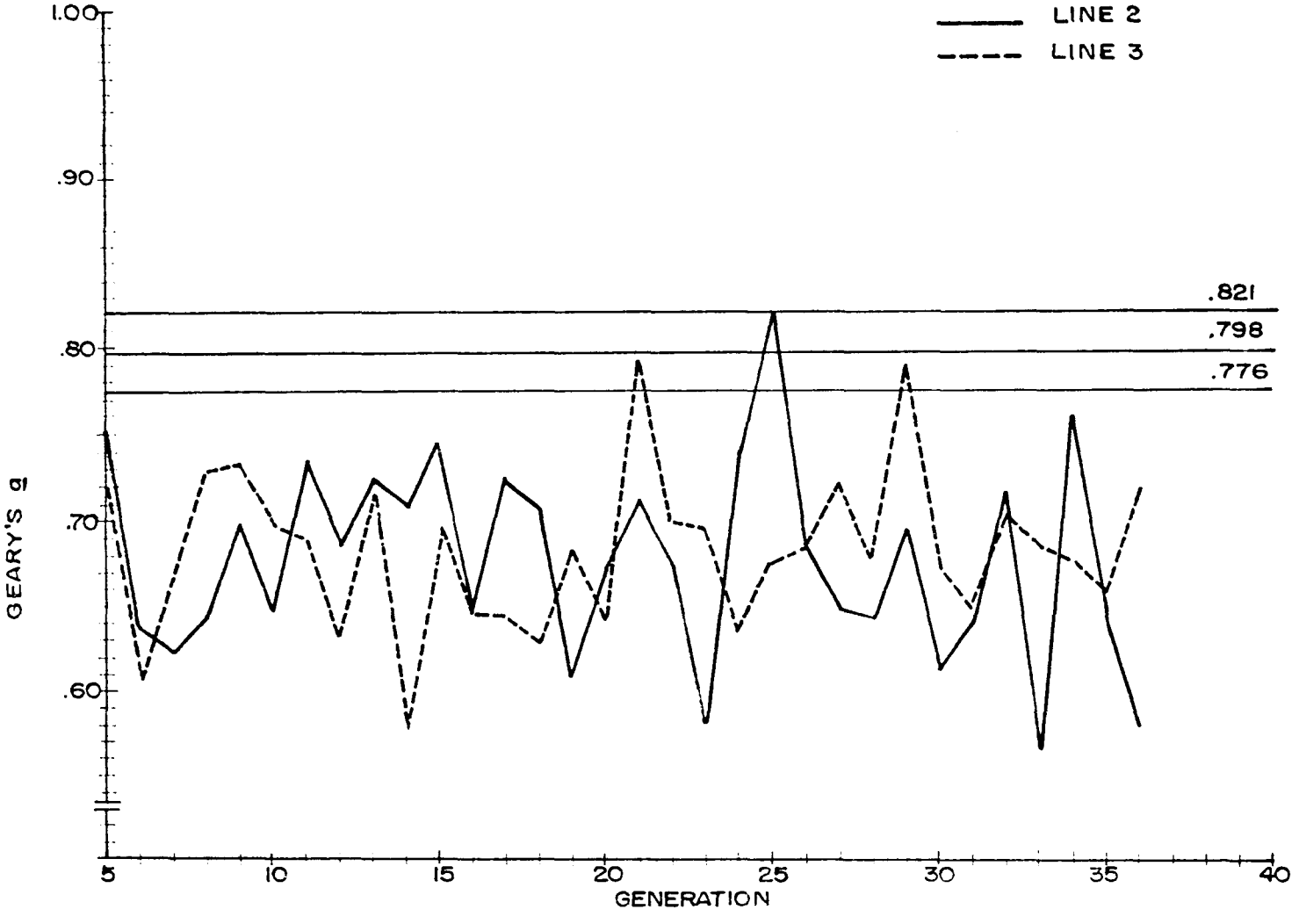


FIGURE 12. VALUES OF GEARY'S a FOR INBREEDING COEFFICIENTS FOR LINES 2 AND 3, GENERATIONS 5 THROUGH 36

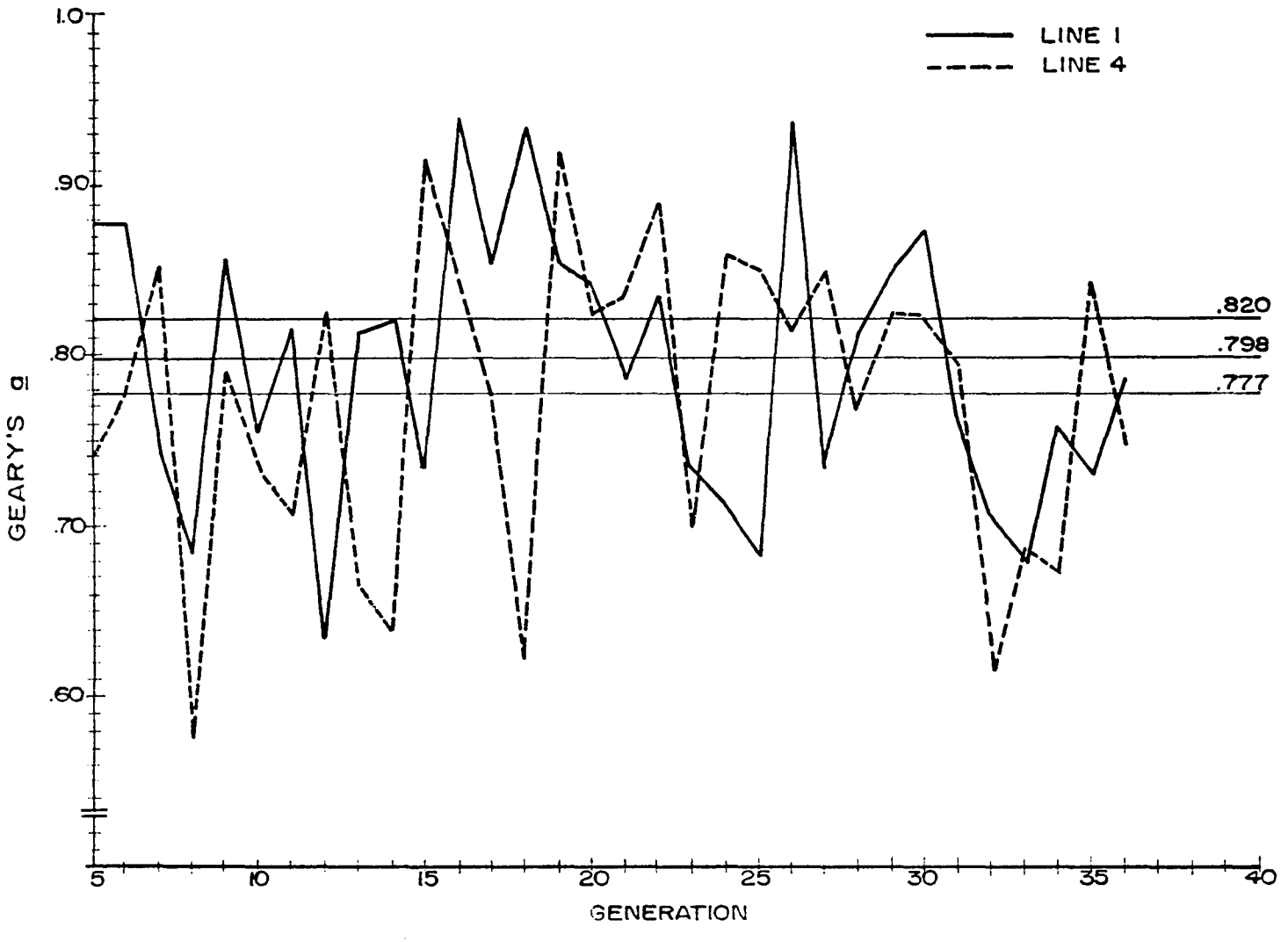


FIGURE 13. VALUES OF GEARY'S a FOR INBREEDING COEFFICIENTS FOR LINES 1 AND 4, GENERATIONS 5 THROUGH 36

decreased over time. Distributions were positively skewed and generally flattened. High inbreeding values extended far above the mean inbreeding values and usually fewer individuals were close to and far from the mean than if the distributions were normal.

In the selected lines, on the other hand, both the range of inbreeding values and coefficients of variation of inbreeding decreased over time. Coefficients of variation were greater in control than in selected lines. The degree of positive skewness was generally smaller in the selected than in the control lines. Distributions were flattened during early and late generations but often peaked over the intermediate generations.

Shapes of inbreeding distributions (described by the coefficient of skewness and Geary's a) within selected and control lines may have been dependent partly upon the rate of inbreeding which, in turn, was dependent upon the mating system. Lines with similar rates of inbreeding had similarly shaped distributions. In the control lines, there were no major changes in rates of inbreeding or in shapes of inbreeding distributions over time. In the selected lines, beginning around G_{15}, distributions tended to become more peaked and less skewed. After selection was relaxed in line 1 and line 4, the distributions returned to near original shapes and the rates of inbreeding in lines 1 and 4 decreased by 52 to 80 percent respectively. This decrease in inbreeding rate may have accounted for the change in the shapes of the distributions after relaxed selection in the selected lines. The

initial shape changes around G_{15} were not associated with large changes in inbreeding rate, however. Magnitude of inbreeding may have affected the shape of the inbreeding distributions because shape (skewness and kurtosis Figures 10 through 13) changed greatly only in the selected lines and only after the mean percent inbreeding exceeded the maximum mean inbreeding attained in the controls (approximately 13 percent).

Responses of Traits to Inbreeding

Estimates Based Upon Within-generation Linear and Quadratic Regressions

Linear and quadratic regressions of each of the eight traits previously defined (Y's) on individual bird coefficients of inbreeding (X) were run by line within generation for G_5 through G_{36} (32 generations). Linear regression coefficients were tested for significance as were the relative improvements of the quadratic over the linear models. The within-generation regression of TW on inbreeding is shown in Figure 14 for G_{20} for example. TW decreased 0.17 grams per one percent increase in inbreeding but this decrease was not significantly different from zero.

Within-generation linear regression coefficients varied considerably in sign and magnitude for all traits within all lines and, therefore, are not presented. Some positive and some negative linear regression coefficients were obtained for each trait within each line. The number of positive and negative coefficients were approximately equal in most cases. The number of significant linear regression coefficients varied from zero

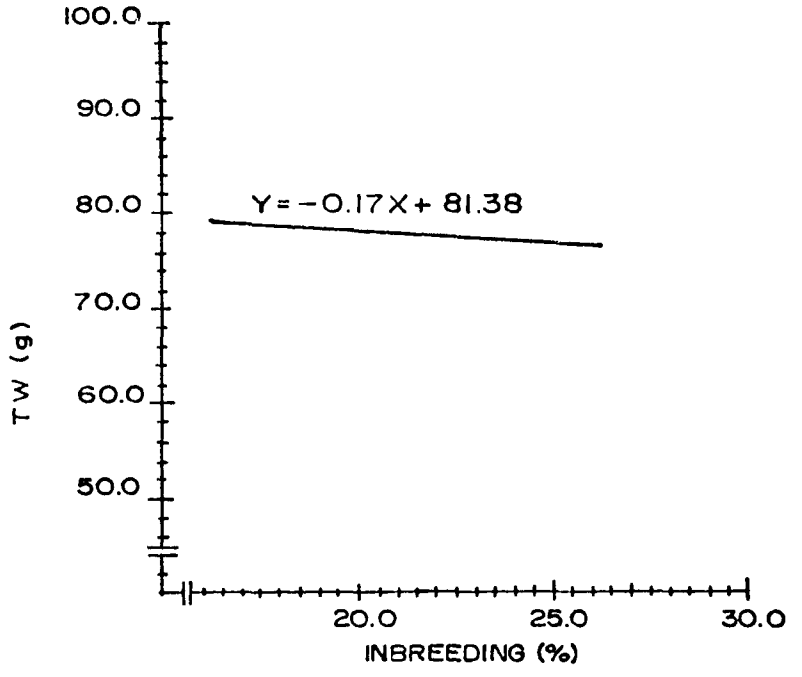


FIGURE 14. WITHIN-GENERATION LINEAR REGRESSION OF TW ON INBREEDING FOR INDIVIDUALS IN LINE 1, G_{20}

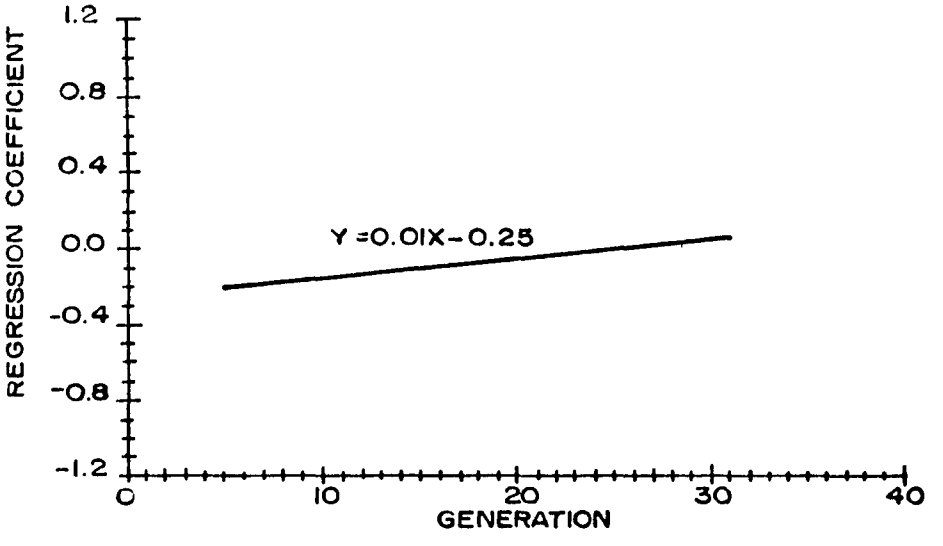


FIGURE 15. REGRESSION OF WITHIN-GENERATION LINEAR REGRESSION COEFFICIENT FOR TW ON GENERATION NUMBER FOR LINE 1, G_5 THROUGH G_{36}

to 12 out of 32 coefficients for each trait within each line. Only for TW, were more than four significant coefficients found within each line. All 12 significant coefficients for TW in line 4 were negative and eight out of 10 were negative in line 1. Therefore, within generations there was some tendency for the more highly inbred individuals to weigh less at three weeks of age in the selected lines. Five out of nine significant coefficients for TW were negative in line 2 and four out of five in line 3. Five out of nine coefficients were negative for AW in line 4 showing no definite trend for this trait.

The linear regression model was generally a better fit than the quadratic model for the regressions of a trait on inbreeding within generations. The quadratic model was significantly better than the linear most frequently for TW, AW and EW. The range of inbreeding values within any one generation (usually less than 10 percent) was too small to permit generalization regarding the direction of the change in response to inbreeding of any of these traits as the level of inbreeding increased.

Linear regressions of the above within-generation linear regression coefficients on generation number were run for each trait within each line, the objective being to determine if the effects of inbreeding on any trait changed during later generations as inbreeding level increased. An example of this type of regression is shown in Figure 15 for TW in line 1 for G_5 through G_{36}. The regression coefficient, 0.01, was not significant indicating that regression coefficients (estimates of the effects

of inbreeding on TW) had not changed significantly over time in line 1. The majority of these regression coefficients obtained in this experiment were non-significant which showed that within-generation regression coefficients for most traits and the effects of inbreeding on these traits had not changed significantly over time within a line. Significant negative regression coefficients were obtained, however, for HFE, HTE and FS in line 3 and FE in line 2 revealing that inbreeding in these lines had a greater depressing effect on these traits in later than in early generations.

Estimates Based Upon Pooled Linear Regressions

Pooled linear regression coefficients were used to estimate the average effects of inbreeding on each of the eight traits within a line. Within-generation corrected sums of squares ($\Sigma x^2, \Sigma y^2$) and corrected sum of cross-products (Σxy) obtained from the linear regression of trait values (Y's) on inbreeding coefficients (X), were pooled across generations within a line for a given trait. Effect of inbreeding on a particular trait estimated within a generation is independent of variation in mean trait value between generations due to selection or changes in the environment. Pooled linear regression coefficients are presented in Table 6 for each of the eight traits. Coefficients from this table are discussed for each trait separately in the following paragraphs.

Three week body weight (TW)

TW decreased significantly by 0.18 and 0.17 grams per

Table 6. - Linear regression coefficients based on pooled sums of squares and crossproducts from the within-generation regression of eight trait values on inbreeding coefficients for lines 1 through 4 for G_5 through G_{36}

Trait	Line				Average pooled b's		
	1	4	2	3	Selected lines	Control lines	All lines
3-week body wgt. (g)	-0.18*	-0.17*	-0.07*	-0.06	-0.18	-0.07	-0.12
Adult body wgt. (g)	-0.17	-0.13	-0.12	-0.22	-0.15	-0.17	-0.16
Egg wgt. (g)	-0.02	-0.02	-0.00	-0.03*	-0.02	-0.02	-0.02
Egg production (eggs)	-0.47*	-0.00	-0.23	-0.07	-0.24	-0.15	-0.19
Fertility (%)	-0.63	0.25	0.05	-0.56	-0.19	-0.26	-0.22
HFE (%)	-0.66	-0.38	-0.14	-0.76	-0.52	-0.45	-0.49
HTE (%)	-0.32	-0.43	-0.25	-0.49	-0.38	-0.37	-0.37
Family size (chicks)	-0.17*	-0.02	-0.08	-0.11	-0.10	-0.10	-0.10

* $P \leq 0.05$

one percent increase in inbreeding in lines 1 and 4, respectively. Decreases in TW of only 0.07 grams (significant) and 0.06 grams (non-significant) were observed in the control lines. Depression of TW may have been less in the controls than in the selected lines because both the rate and ultimate level of inbreeding were lower in the controls. The lower rate of inbreeding in the controls would have permitted elimination through natural selection of more individuals possessing deleterious recessives than in the selected lines thus countering inbreeding depression (Falconer, 1960). Sittmann et al. (1966) reported an average decrease in body weight at six weeks of age for males and females together of 0.3 grams per one percent increase in inbreeding.

Adult body weight (AW)

AW decreased 0.17 and 0.13 grams (non-significant) per one percent increase in inbreeding in lines 1 and 4, respectively. Control lines showed non-significant decreases in AW of 0.12 and 0.22 grams. AW declined 0.16 grams per one percent increase in inbreeding on the average over all lines. Shinjo et al. (1971) reported an average decrease in 16-week body weight for males and females together of 0.10 grams per one percent increase in inbreeding.

Mean egg weight (EW)

Depression of egg weight with increased inbreeding was minimal and non-significant in all lines. The average decrease in egg weight was 0.02 grams per one percent increase in inbreeding. Coefficients for the regression of egg weight on inbreeding reported by Shinjo et al. (1971) and Kawahara (1972)

averaged 0.01 grams.

Egg production (EP)

EP declined significantly (-0.47 eggs) with increased inbreeding in line 1. EP was not affected by inbreeding in line 4. The effect of inbreeding on EP in the control lines was also not significant. Genes deleterious to egg production may have been in greater frequency in line 1 than in the other lines. Sittmann et al. (1966) and Shinjo et al. (1971) reported decreases in EP of 0.15 and 0.17 eggs (non-significant) per one percent increase in inbreeding, respectively. The average decrease in EP over all lines in this experiment was 0.19 eggs per one percent inbreeding.

Fertility (FE)

Decreases in FE with increased inbreeding were non-significant regardless of the line but the magnitude and direction of the effects varied between lines. Decreases of 0.6 percent per one percent increase in inbreeding were observed in lines 1 and 3. FE increased by 0.25 percent per one percent increase in inbreeding in line 4 and by 0.05 percent in line 2. In lines 2 and 4, genes causing unfavorable interactions may have been eliminated or certain deleterious dominant genes may have been reduced in frequency by inbreeding. Sittmann et al. (1966) and Kawahara (1972) reported decreases in fertility of 1.1 and 0.9 percent per one percent increase in inbreeding, respectively, while Shinjo et al. (1971) and Shinjo et al. (1972) found decreases of 0.4 and 0.6 percent, respectively.

Hatchability of fertile eggs (HFE)

HFE decreased with increased inbreeding in all lines but the decreases were not significant. Decreases in HFE were greatest in lines 1 and 3 and least in line 2. Lines 1 and 3 responded to inbreeding similarly for HFE and FE and these lines may possess deleterious genes which have mutual effects upon FE and HFE. The average decrease in HFE for lines 1 and 3 was 0.7 percent per one percent increase in inbreeding. This was the value obtained by Sittmann et al. (1966), but Shinjo et al. (1971), Kawahara (1972) and Shinjo et al. (1972), obtained values of -0.6, -1.1 and -0.9, respectively.

Hatchability of total eggs (HTE)

HTE is a composite trait reflecting the effects of inbreeding on both FE and HFE. The regression coefficients were remarkably uniform in magnitude from line to line, in contrast to coefficients for FE and HFE. The average decrease in HTE per one percent increase in inbreeding for the four lines was 0.37 percent.

Family size (FS)

FS was dependent upon the rate of egg production during the period that eggs were being saved, and upon FE and HFE. Lines 1 and 3 showed the most rapid declines in FS upon inbreeding. The relatively large declines in FE and HFE with inbreeding in these two lines probably explain the large decreases in FS. It is interesting to note, however, that in line 1 the decrease in EP with inbreeding was statistically significant. Rate of production in this line during the time that eggs were being saved

declined significantly with inbreeding and could have influenced FS as did FE and HFE. The decreases in FS in lines 4 and 2 of 0.02 and 0.08 chicks per one percent increase in inbreeding, respectively, were relatively small. Moreover, FE was not affected by inbreeding in either line 4 or line 2 and HFE decreased less upon inbreeding in these lines than in lines 1 and 3.

Summary of Trait Responses to Inbreeding as Estimated by Pooled Regression

Traits varied in their responses to inbreeding as measured by pooled regressions of trait value upon unit level of inbreeding. Traits normally having relatively high heritability (TW, AW and EW), presumably with corresponding low levels of dominance variance, were little depressed by inbreeding. This was expected since depression of a trait value with inbreeding depends upon loss of dominance among alleles affecting that particular trait (Crow, 1952). Decreases in FS were also very small with increased inbreeding. On the other hand, traits having low heritability (HFE, HTE and FE) were substantially depressed by inbreeding.

Response to inbreeding also varied among lines. Average decreases in AW, EW, HTE and FS with increased inbreeding (Columns 5 and 6, Table 4) were similar in both the selected and the control lines. The selected lines, however, showed somewhat larger decreases, on the average, with inbreeding in TW, EP and HFE than did the control lines. FE was the only trait for which inbreeding depression was much greater in the control lines than in the selected lines. Line 3 showed much greater inbreeding

depression for AW than did the other lines. Lines 1 and 2 showed the greatest decreases in EP with inbreeding. Lines 1 and 3 showed the greatest declines upon inbreeding in FE, HFE and FS. Trait values declined least in line 2 for five of the eight traits studied.

Declines in TW and AW with inbreeding averaged over all lines were less than those obtained by Sittmann et al. (1966) for six week body weight but approximately the same as those reported by Shinjo et al. (1971) for 16-week body weight. Declines in these traits for any particular line were never as great as that reported by Sittmann et al. (1966). In the experiments cited for comparison with the regression results obtained here, inbreeding was rapid (i.e., by continuous full-sib matings for up to five generations or approximately 13.4 percent increase in inbreeding per generation). Inbreeding depression was expected to be less in this experiment where rates of inbreeding were lower (up to 1.5 percent per generation) because natural selection over more generations would tend to eliminate individuals possessing deleterious combinations of genes (Falconer, 1960).

Declines in FE and HFE averaged over all lines were also less than reported values presented in Table 1. For each of these traits, however, at least one line in this experiment was found in which inbreeding depression was greater than that observed in an experiment involving consecutive full-sib matings. Declines in EP and EW averaged over all lines were very close

to reported values in Table 1 but again some lines in this experiment showed greater inbreeding depression for these traits. Estimates of the effects of inbreeding on HTE and FS in quail apparently have not been reported.

GENERAL DISCUSSION

Inbreeding depressed trait values in quail for all traits in most lines in this experiment. Trait responses to inbreeding, however, varied considerably between lines. It may be possible, therefore, to form inbred lines of quail by selecting from a large population of inbred lines derived from one base population those least sensitive to inbreeding depression in fitness traits. Concurrent selection for improved performance in economic traits may aid in reducing or preventing inbreeding depression. Three week body weight increased by an average of 1.13 grams per generation during the first 25 generations of selection, for example, despite mean inbreeding coefficients up to 34 percent (Unpublished data [1975] from W. M. Collins, Dept. of Animal Sciences, Univ. of New Hampshire, Durham, N. H.).

Response to inbreeding of each trait studied in this experiment, averaged over all lines, is shown in column seven of Table 6. Where possible, these were compared with coefficients obtained for chickens given in Table 1. Estimates of inbreeding depression for egg production and body and egg weight in chickens were based upon a greater number of generations and upon a much heavier bird and egg, respectively, than in quail. Hatchability declined less with inbreeding in chickens than in quail.

A rough estimate of the relative proportion of individuals with different degrees of inbreeding may be obtained from

knowledge of the shape of a distribution of inbreeding coefficients. Distribution shape might be predictable from inbreeding rate. In this experiment, lines with higher rates of inbreeding had distributions of inbreeding coefficients within generations whose shapes more closely approached normality. Individuals were distributed more equally above and below the mean percent inbreeding in the selected lines. Rate of inbreeding in the selected lines was as great as 1.5 percent per generation during selection. There were always more individuals less inbred than the mean percent inbreeding in distributions of inbreeding coefficients in the control lines. Rate of inbreeding in the control lines averaged only 0.4 percent per generation. Practical application of inbreeding distribution shape is not evident since individuals with low inbreeding do not necessarily produce offspring with low inbreeding or with superior performance for a particular trait.

Inbreeding coefficients calculated for each line each generation probably were lower than actual inbreeding coefficients. The major reason for this belief is that inbreeding in the base generation was assumed to be zero but the population likely was inbred before the lines were formed and selection begun. Moreover, high levels of linkage between genes, if present, would tend to increase actual inbreeding above calculated values because more than one locus would become homozygous simultaneously within an individual (Bogyo and Ting, 1968). Mutation might, on the other hand, bias calculated inbreeding upward (Falconer, 1960) but mutation rates are normally very low

and, therefore, would likely have little influence on inbreeding rate over the 36 generations studied.

CONCLUSIONS

1. Inbreeding accrued more rapidly under family selection than under random mating *per se*.
2. Avoidance of full-sib matings was especially effective in reducing rate of inbreeding in lines undergoing family selection.
3. The coefficient of variation of inbreeding coefficients declined with increasing inbreeding.
4. Distributions of coefficients of inbreeding appeared to deviate farther from normality in the lines with lower rates of inbreeding.
5. It may be possible to estimate shapes of distributions of inbreeding coefficients from knowledge of inbreeding rates.
6. Response to inbreeding appeared to be unique to a line.
7. Low rates of inbreeding (0.3 to 1.5 percent per generation) over 36 generations sometimes reduced average response of a trait to inbreeding below that observed by other workers where consecutive full-sib mating was practiced for three to five generations and the rate of inbreeding ranged from 13.4 to 16.7 percent per generation.
8. TW, AW and EW, traits of high heritability, generally declined more slowly with inbreeding than traits of low heritability such as HFE, HTE and FE.

SUMMARY

The four quail lines involved in this study differed significantly from one another in rate and magnitude of inbreeding. Inbreeding accrued about three times more rapidly in the selected lines than in the control lines. During relaxed selection rate of inbreeding declined from 1.2 to 0.6 percent per generation in line 1 and from 1.5 to 0.3 percent in line 4.

In the control lines, the theoretical rate of inbreeding estimated from effective population number was similar to calculated inbreeding rate based upon the variance-covariance method. In the selected lines, however, the theoretical inbreeding rate was 0.20 and 0.28 percent per generation greater than that calculated for lines 1 and 4, respectively. The large differences between theoretical and calculated rates in the selected lines were attributed to a greater avoidance of full-sib mating in these lines than in the control lines.

Distributions of inbreeding coefficients were skewed positively and flattened in all generations in the control lines and in the early and late generations in the selected lines, i.e., most individuals had inbreeding coefficients less than the mean coefficient of inbreeding. Distributions more closely approached normality in the selected lines and became less positively skewed and often peaked during intermediate generations. Distribution shape was similar for lines with similar rates of inbreeding and followed changes in inbreeding rates in

the selected lines.

Regression coefficients for within-generation linear regressions of trait values on inbreeding for each trait and line varied substantially from generation to generation. Rarely, however, did coefficients for a particular trait and line show a significant increase or decrease over time. The change in performance with inbreeding for each trait within each line was obtained as a linear regression coefficient for regression of trait value on inbreeding pooled over all generations. The degree of inbreeding depression for a given trait varied widely among lines. Each trait except FE, however, decreased in value with inbreeding in each line but few pooled regression coefficients were significant. Performance was usually depressed least in control line 2 and for traits of high heritability (TW, AW and EW). Average response to inbreeding for each trait in the selected lines was generally little different from that in the control lines despite lower rates of inbreeding in the control lines. Pooled regression coefficients for each trait averaged over all lines were generally similar to or smaller than regression coefficients for the same trait reported in other studies in which rates of inbreeding were much higher than those found here.

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BIOGRAPHICAL DATA

Name in Full — John William Hardiman

Date of Birth — January 18, 1949

Place of Birth — New York, New York

Secondary education — Huntington High School
Huntington, Long Island, New York

Collegiate Institutions attended	Dates	Degrees
State University of New York College at Cortland	1966-1970	B.A. (Biology)
University of New Hampshire	1971-1975	Ph.D. (Genetics)

Honors or Awards

New York State Regent's Scholarship
George Dwinell Fund
Graduate Research Assistantship
Hubbard Fellowship

Publications

Collins, W. M., J. W. Hardiman, W. E. Urban, Jr. and A. C. Corbett. Genetic differences in susceptibility to ulcerative enteritis in Japanese quail (to be published in Poultry Science).

Hardiman, J. W., W. M. Collins and W. E. Urban, Jr. 1974. A red egg shell mutant in Japanese quail. Poultry Sci. 53:1932. (Abstr.)

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Hardiman, J. W., W. M. Collins and W. E. Urban, Jr. 1975. Red egg shell color: a dominant mutation in Japanese quail. J. Hered. 66:141-143.

Position held	Dates
Graduate Research Assistant Dept. of Animal Sciences University of New Hampshire Durham, New Hampshire	1973-1975